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Shrub Response to Forest Restoration and Fuels  
Management Treatments

**FINAL REPORT**

**SHRUB RESPONSE TO FOREST RESTORATION AND FUELS MANAGEMENT  
TREATMENTS**

**RMRS-99167-RJVA**

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## Preface

The following is the final report for a joint venture research agreement between United States Forest Service, Rocky Mountain Research Station and Northern Arizona University (NAU), School of Forestry (RMRS-99167-RJVA). This work was also conducted as partial fulfillment of the School of Forestry and NAU Graduate College requirements for the degree of Ph.D. (Forest Science). Project objectives were modified over the course of the four-year study period in relation to resource availability, logistical constraints, and data findings. Two species, *Ceanothus fendleri* and *Rosa woodsii* were selected for study, although readers will find our research effort was weighted toward studies of *C. fendleri*. This unequal effort developed from purely logistical reasons and in no way suggests ranking of ecological importance between the two species.

## Publications

- Huffman, D.W. *In Prep.* Population ecology of *Ceanothus fendleri*: effects of forest restoration treatments and herbivory in a ponderosa pine forest of northern Arizona. Ph.D. Dissertation. Northern Arizona University, Flagstaff, AZ.
- Huffman, D.W., and M.M. Moore. 2003. Ungulate herbivory on buckbrush in an Arizona ponderosa pine forest. *Journal of Range Management In Press*.
- Huffman, D.W. 2002. A seed chalcid (*Eurytoma squamosa* Bugbee) parasitizes buckbrush (*Ceanothus fendleri* Gray) seeds in a ponderosa pine forest of Arizona. *Western North American Naturalist* 62:474-478.

## Presentations

- Huffman, D.W., and M.M. Moore. 2002. Effects of restoration treatments and herbivory on buckbrush (*Ceanothus fendleri* Gray). Oral presentation -- Society for Range Management Annual Meeting, Flagstaff, Arizona.
- Huffman, D.W., and M.M. Moore. 2002. Response of buckbrush (*Ceanothus fendleri* Gray) to overstory thinning and prescribed fire. Oral presentation -- Ecological Society of America Annual Meeting, Tucson, Arizona.
- Huffman, D.W., and M.M. Moore. 2000. Herbivory on *Ceanothus fendleri*: Implications for forest restoration. Poster presentation -- Ecological Society of America Annual Meeting, Snowbird, Utah.

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## Executive Summary

Many ponderosa pine forests in the Southwest region of the United States are overly dense and in a state of ecological degradation. In order to reduce catastrophic fire hazard and bring about more natural ecosystem function, ecological restoration treatments that include tree thinning and prescribed fire are underway. In these forests, ecological responses of common plant species, particularly shrubs, to thinning and prescribed fire have been minimally researched. Furthermore, the role of herbivory in constraining species responses has not been adequately addressed. To determine the effects of restoration thinning, prescribed fire, and herbivory on selected understory shrubs, we monitored populations of *Ceanothus fendleri* Gray (buckbrush) and *Rosa woodsii* Lindl. (woods rose) over four years (1999-2002). We conducted several experimental and observational studies to quantify growth, sprouting potential, reproduction, and herbivory in treated and untreated overstory units. Results indicated generally positive responses of both species to thinning and burning treatments. Important findings were the following:

- 1) *C. fendleri* growth was negatively related ( $p < 0.001$ ) to overstory density but little variation was explained by stand density ( $r^2 = 0.23$ ; Reineke's Stand Density Index);
- 2) Models explaining *C. fendleri* growth were improved by adding measures of current-year herbivory ( $r^2 = 0.47$ );
- 3) Individuals of both *C. fendleri* and *R. woodsii* grew significantly ( $p < 0.05$ ) larger when protected from large herbivores. Protected *C. fendleri* stems in treated overstory units were larger than unprotected stems (1999 and 2000) by approximately two-fold. Protected *R. woodsii* stems were nearly 50% taller than unprotected stems (2001).
- 4) Flowering *C. fendleri* stems were found on a significantly ( $p < 0.05$ ) greater proportion of plots protected from herbivores than plots not protected. On protected plots, *C. fendleri* plants produced 1.9-35 seeds per reproductive stem; on plots not protected from herbivores, *C. fendleri* stems did not produce fruits or seeds. We did not observe flowering of *R. woodsii* plants during the four years.
- 5) Seeds produced by *C. fendleri* were parasitized by a chalcidoid wasp (*Eurytoma squamosa* Bugbee). Parasitism was responsible for loss of 9-50% of otherwise normally developed *C. fendleri* seeds.
- 6) Seed predators removed 1.3-24.3% of *C. fendleri* and *R. woodsii* seeds experimentally placed along transects on charred forest floor and ponderosa pine needle substrate. No significant ( $p > 0.05$ ) differences in mean removal rate between species were found. In 2001, significantly ( $p < 0.05$ ) more *C. fendleri* seeds were removed from charred forest floor than pine needle substrate.
- 7) Forest floor depth consumed in prescribed fires was significantly ( $p < 0.05$ ) related to probability of *C. fendleri* mortality and seedling emergence from soil seed banks. *C. fendleri* seed germination experiments corroborated findings from field plots. Germination was significantly greater for seeds heated for 10 minutes at 90° C than seeds that were not heated. Temperatures of 130° C or greater killed *C. fendleri* seeds. Just two of 36 *R. woodsii* plants were killed by fire. Surviving plants of *C. fendleri* and *R. woodsii* resprouted from stem bases and belowground structures. Stems produced by *C. fendleri* in response to fire were typically long with few branches. *R. woodsii* plants in thinned and burned units were not significantly different ( $p > 0.05$ ), in terms of stem height or number of stems, from plants in untreated control units (2001).

Results of our studies demonstrate that *C. fendleri* and *R. woodsii* are integral components of ponderosa pine forest ecosystems. Both species provide important habitat qualities for a myriad of organisms within the food web. Restorative treatments such as tree thinning to reduce wildfire hazard and competitive effects on understory communities, and applications of prescribed fire to reduce accumulated fuel loads and reintroduce a critical ecosystem process, by enhancing growth and reproduction of important plant species such as *Ceanothus fendleri* and *Rosa woodsii*, help to return ecological function to these forests.

## Introduction

Ponderosa pine (*Pinus ponderosa* Laws.) forest ecosystems of the southwestern United States have experienced a population irruption of small trees over the last century and have become correspondingly dense (Covington and Moore 1994a, Covington and Moore 1994b, Covington et al. 1997, Moore et al. 1999). Livestock grazing, fire suppression, and selective logging associated with Euro-American settlement in the late 1800s and early 1900s favored the establishment of pine regeneration, which occurred in pulses of anomalous magnitude (Savage et al. 1996). Continued suppression of the indigenous fire regime, one in which surface fires burned through bunchgrass, forb, and shrub understories at intervals of two to five years (Fulé et al. 1997), allowed persistence of young trees and development of dense forest stands. Current forest conditions are responsible for many critical conservation problems, including loss of native species diversity, declining herbaceous and tree productivity, and high-mortality of old-growth trees (Kolb et al. 1994, Biondi 1996, Mast et al. 1999). In addition, these forests are now exposed to increased risk of stand replacing crown fire due to extreme levels of accumulated woody fuels (Covington and Moore 1994a). Thus, in many areas, southwestern ponderosa pine forests are in a state of ecological degradation and in need of restorative treatments (Kolb et al. 1994).

Basic concepts of the science of ecological restoration include reversing deleterious changes and restoring ecosystems to more nearly natural conditions (Society for Ecological Restoration 1993). Restoration treatments in southwestern ponderosa pine forests include intensive thinning to restore forest structure and prescribed fire to reduce accumulated woody fuels and reintroduce an important ecological process (Covington et al. 1997, Moore et al. 1999). Past studies of understory plant response to tree thinning and fire in southwestern ponderosa pine ecosystems have mainly focused on forage production, which tends to increase after tree thinning or as overstory density decreases (Ffolliott and Clary 1975, Bojorquez Tapia et al. 1990, Moore and Deiter 1992) and increases after fire (Arnold 1950, Pearson et al. 1972, Patton 1974, Andariese and Covington 1986, Vose and White 1991). However, little autecological detail exists regarding responses of common plant species, particularly shrubs, to forest management. Furthermore, the role of herbivory in constraining understory species response in these ecosystems has not been adequately addressed.

## Objectives

The overall objective of this research was to provide basic autecological information for common shrubs with a focus on plant response to overstory thinning, season of prescribed fire, and herbivory. The project was designed with detail and depth appropriate to fulfill the partial requirements of a Ph.D. dissertation. Field experiments were employed to examine plant growth and vigor following restoration treatments in the Fort Valley portion of the Flagstaff Urban-Wildland Interface.

The specific objectives of this study were as follows:

1. Determine the effects of restoration treatments (specifically thinning and prescribed fire) and herbivory on selected understory shrubs
2. Quantify the phenology and physiology of the selected understory shrubs in restoration treatments
3. Quantify ovule and seed fate of shrubs in units thinned for ecological restoration

## Background and Literature Review

### Study Species

Two species, *Ceanothus fendleri* Gray (buckbrush) and *Rosa woodsii* Lindl. (formerly, *R. arizonica*; Arizona wild rose) are common shrubs found throughout northern Arizona ponderosa pine forests. These species are excellent subject species for population studies due to their abundance in understory communities. Additionally, these species provide important ecosystem functions. For example, *C. fendleri* is actinorhizal and

capable of dinitrogen-fixation (Story 1974). Capture and eventual addition of N to soils creates a more favorable environment for establishment and growth of other plants and soil organisms. Story (1974) estimated N-fixation of *C. fendleri* to be around 0.12 kg/ha/y. *C. fendleri* is also an important browse species for mule deer (*Odocoileus hemionus*) (Urness et al. 1975) and may also be used by elk (*Cervus elaphus*). In Beaver Creek watershed in northern Arizona, Urness et al. (1975) found that *C. fendleri* constituted a significant portion (1.4 – 6.9%) of the summer browse of mule deer, surpassed only by Gambel oak (*Quercus gambelii*), mountain mahogany (*Cercocarpus brevifolia*), and ponderosa pine. *Rosa woodsii* is also browsed by mule deer (Austin and Hash 1988). Both the new leaves as well as the “hips” (fruits) are used. Fruits of *Rosa woodsii* are an important winter food source for many species of wildlife (Blauer et al. 1975, Welch and Andrus 1977). In addition to wildlife benefits, *R. woodsii* has human uses such as revegetation of road cuts and phytochemicals. Both shrubs provide structure heterogeneity in predominantly herbaceous understories.

## Effects of Thinning

Similar to other ecosystems, production of understory communities in ponderosa pine forests has been found to increase after overstory thinning and decreases in stand density (Ffolliott and Clary 1975, Bojorquez Tapia et al. 1990, Moore and Dieter 1992). However, few autecological details exist regarding plant responses to thinning. For example, length of shoots of *C. fendleri* produced after thinning has not been quantified. Similarly, demographic dynamics of stem populations in contrasting environments has not been described. Biomass estimates of *C. fendleri* have been made at the plot level from visual estimates of plants comprising stems of all ages (Vose and White 1991). However biomass of new growth based on shoot characteristics and changes associated with thinning have not yet been quantified. We are not aware of studies reporting response of *R. woodsii* to overstory treatments.

## Role of Fire

Fire plays an important ecological role in southwestern ponderosa pine forests. It has been shown that forage biomass in these ecosystems tends to increase after fire (Arnold 1950, Pearson et al. 1972, Patton 1974, Andariese and Covington 1986, Vose and White 1991). Although resprouting of *Ceanothus fendleri* has been documented, little detail is available concerning fire effects on population structure or growth (Pearson et al. 1972, Ffolliott et al. 1977). Recovery of *C. fendleri* biomass has been found to vary with stand type (e.g., sawtimber, pole, sapling) (Vose and White 1991). One year after a prescribed burn in northern Arizona, *C. fendleri* biomass was reduced in below-canopy sawtimber stands but was not reduced in open sawtimber (Vose and White 1991). Burn intensity probably accounts for these differences but there are no data to support this speculation. In the mixed conifer forests in the Sierra Nevada Range, sprout number of *Ceanothus cordulatus* (whitethorn) increased for two years after prescribed fire whereas height and basal diameter of sprouts initially decreased (Kauffman and Martin 1990). Similarly, cover of *Ceanothus velutinus* (snowbrush) in Idaho was lower in burned aspen (*Populus tremuloides*) and aspen-conifer mixed forest plots compared with unburned plots (Brown and DeByle 1989). Noste (1985) found that fire season affected cover response of *C. velutinus* and that mortality was greater after hot fall fires (60%) than those (0%) that burned cooler in spring. Fire can affect demography of clones and populations as stems are killed and new sprouts are recruited. For example, after producing an initial flush of new stems following disturbance, other shrub species have been shown to persist by annually recruiting stems into local populations (Tappeiner et al. 2001). This eventually leads to an all-aged stem population structure. However, studies of aerial stem dynamics after disturbance and under various forest conditions have not been conducted for *Ceanothus fendleri*. Fire can also influence clone morphology although this has not been quantified for *C. fendleri*. Throop and Fay (1999) found long unbranched ramets produced by burned *Ceanothus herbaceous*, a species with a growth form similar to *C. fendleri*, whereas unburned plants were heavily branched with shorter shoots. Morphological responses such as these may provide clues to persistence strategies in an environment characterized by frequent fire. Research at the species' population level has shown response pathways that vary from positive to negative in terms of survival of individuals, biomass production, and seedling recruitment (Vose and White 1987, Vose and White 1991). These responses appeared to be determined by interactions of species' innate characteristics (e.g., morphology) and fire severity.

Seedling establishment may play an important role in the recovery of *C. fendleri* populations following fire. This is true of many *Ceanothus* species (Keeley 1977, Conard et al. 1985, Noste 1985, Throop and Fay 1999). *Ceanothus fendleri* seeds, like those of congeneric species, are reported to need heat scarification plus cold stratification in order to germinate (Story 1974). However, no germination test data have been published. In a field study near Flagstaff, Arizona, a greater number of seedlings were found on plots where adult plants suffered high rates of fire-induced mortality (Vose and White 1987). These data suggest that *C. fendleri* may utilize a buried seed regeneration strategy, however, no seeds were found in seed bank tests (Vose and White 1987). It should be noted that seed bank studies that do not utilize heat treatments would not likely stimulate *C. fendleri* germination. The effects of environmental variables on seedling survival, whether under controlled or field conditions, have not been studied.

Seeds of *Rosa woodsii* also require cold stratification following heat or scarification to germinate (Gill and Pogge 1974). Little is known regarding the contribution of buried seed to population recovery following fire. Vose and White (1987) found an average of less than 0.1 seedlings per square meter after a prescribed burn in a pole stand of ponderosa pine in northern Arizona. Seedling recruitment of a similar species (*Rosa gymnocarpa*) was nil after a duff burn in northern Idaho, although its seeds were found in the seed bank before fire (Morgan and Neuenschwander 1988).

## Role of Herbivory

The role of herbivory in constraining understory development, structure, and responses has not been adequately addressed for southwestern ponderosa pine forests, however, it is widely recognized that large mammalian herbivores, through selective herbivory and physical disturbance to sites, often play key roles in ecosystems and have important effects on community structure, composition, and processes (Anderson and Loucks 1979, Naiman 1988, Augustine and McNaughton 1998). At low levels of herbivory, tolerant plant species may compensate for tissue loss by increasing production of biomass or reproductive structures (Rosenthal and Kotanen 1994, Augustine and McNaughton 1998, Throop and Fay 1999). This can give species preferred by herbivores a competitive advantage and increase their relative abundance in the community. In contrast, high levels of herbivory or repeated defoliation can decrease plant vigor and lead to reduced reproductive output, regeneration failure, or mortality, and thereby benefit non-preferred species (Strohmeyer and Maschinski 1996, Kay 1997, Augustine and Frelich 1998, Augustine and McNaughton 1998, Suzuki et al. 1999, Opperman and Merenlender 2000). Further, herbivory can alter structural characteristics of plants by increasing or reducing overall size and affecting branching patterns and morphology (Debyle 1985, Throop and Fay 1999). In the long term, shifts in community species composition and structural characteristics can affect a broad array of ecosystem processes. The range of potential ecosystem effects make assessment of herbivory particularly important for land management activities such as ecological restoration. Monitoring herbivory and its effects can allow restoration ecologists and resource managers to predict rates and patterns of community development and design adaptive treatment strategies. Intense herbivory has been shown to affect community composition and structure in other ecosystems (Augustine and McNaughton 1998, Augustine and Frelich 1998).

## Methods

### Study Site

The study was conducted 1999-2002 on the Fort Valley Experimental Forest (latitude 35° 16' N, longitude 111° 41' W) in Coconino County approximately 10 kilometers northwest of Flagstaff, Arizona (Fig. 1). The site is located approximately 2300 m above mean sea level and has flat to gently rolling topography with slopes generally less than 20%. Annual precipitation averages 52 cm, of which approximately half falls as snow in late winter. Soils are moderately well drained classified as Brolliar stony clay loam (Meurisse 1971) developed from tertiary basalt parent material.

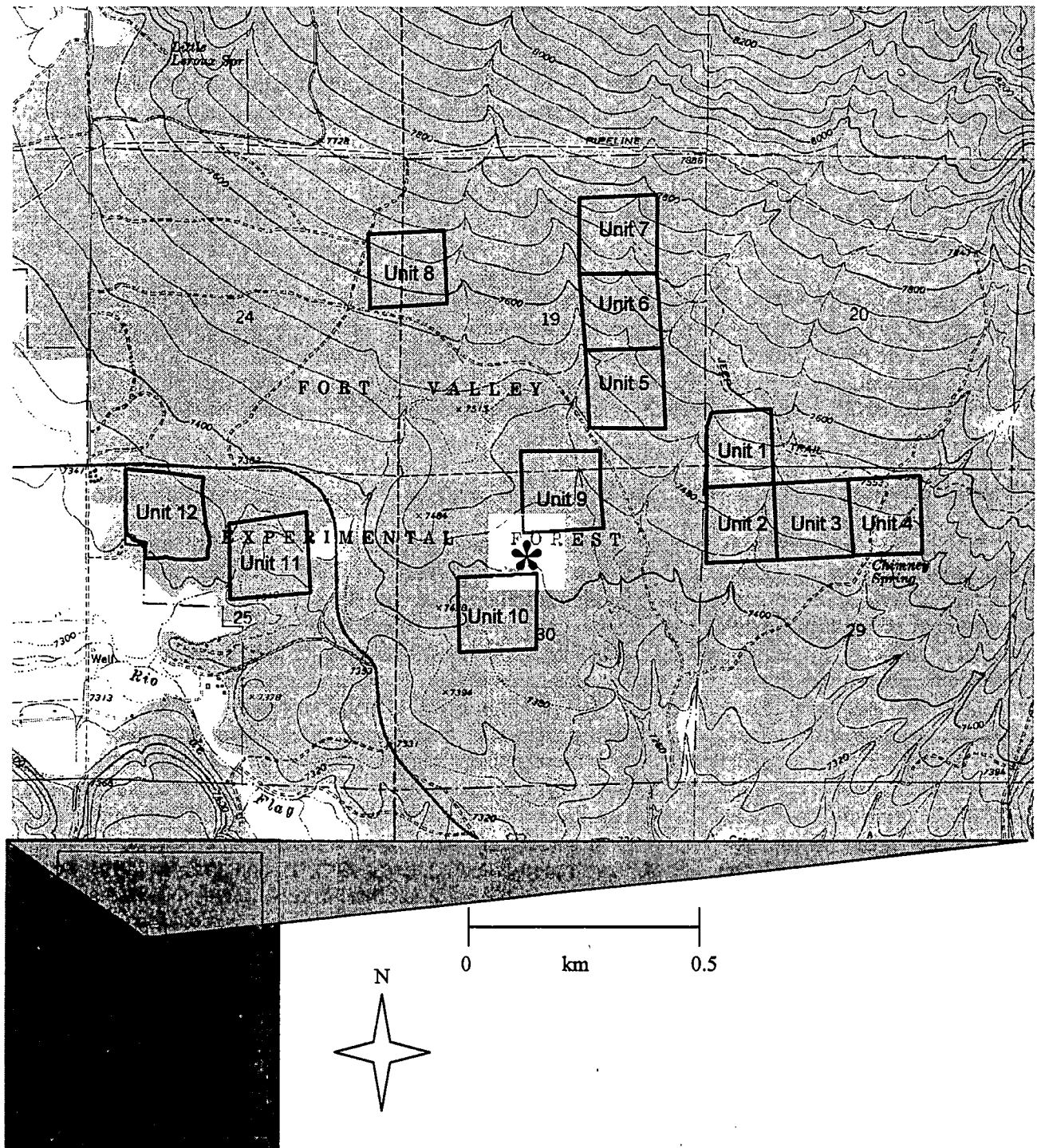


Figure 1. Fort Valley study site in northern Arizona. Treated overstory units used for studies of *Ceanothus fendleri* were 4, 5, and 10. These, and additional treated units 1, 2, and 7, were used for studies of *Rosa woodsii*. Control units used for studies of both species were 3 and 9. An additional control area (10b) was used for studies of *C. fendleri* and is indicated by an asterisk (located above unit 10).

Overstory vegetation was nearly pure ponderosa pine with scattered occurrence of Gambel oak (*Quercus gambelii* Nutt.). Common understory species included bunchgrasses *Festuca arizonica*, *Muhlenbergia montana*, *Elymus elymoides*, and *Blepharoneuron tricholepis*, forbs *Lupinus* spp., *Erigeron* spp., *Eriogonum* spp., *Achillea millifolium*, and *Antennaria* spp., and scattered populations of woody shrubs including *Ceanothus fendleri*, and *Rosa woodsii*.

Large mammalian herbivores were present on the site and include mule deer and elk (*Cervus elaphus*). Domestic livestock were excluded from the study site.

Prior to European colonization of the area in the late 1800's, tree density was around 56 trees per hectare (Covington et al. 1997). Settlement of the area brought intensive livestock grazing and wildfire suppression. Coupled with logging, these impacts allowed the establishment of dense stands of second-growth trees that occur at densities of up to 3,071 trees per hectare (Covington et al. 1997). In presettlement forests, we presume that understory communities were luxuriant assemblages of forbs, grasses and shrubs. However, much of this abundance has been eliminated due to increased overstory density and probably fire exclusion.

In 1998-1999, forest restoration treatments were initiated on around 250 hectares of the study area. The treatments were designed to reduce woody fuel loads, reestablish overstory structure similar to that of presettlement stands, stimulate understory recovery, and reintroduce surface fire as an ecosystem process. Forest treatments in the study area are arranged in three experimental blocks. Each block comprises three overstory prescriptions to test effects of different thinning intensities on an array of forest variables (see Fulé et al. 2001a). Prescriptions were based on the number of post-settlement-aged trees (< 130 years old) left to replace dead presettlement evidence such as snags, stumps, and logs. Replacement of presettlement evidence was meant to reestablish tree spatial arrangements that were present in these forests at time of disruption of natural frequent fire regimes (ca 1870) (Fulé et al. 2001a). In this report, thinning prescriptions are referred to as light (1.5-3 replacements), moderate (2-4 replacements), and heavy (4-6 replacement trees per evidence). In general, mechanical thinning for these treatments reduced overstory densities 80-95% (Fulé pers. comm.) to approximately 60-90 trees per hectare.

## Procedures

Due to time and resource constraints, we were not able to sample both *Ceanothus fendleri* and *Rosa woodsii* with the same intensity. In order to achieve our study objectives and provide detailed information regarding life history, growth, and reproduction given our constraints, we focused the majority of our efforts over the four-year study period on ecological studies of *C. fendleri*.

### Plot Establishment

#### *Ceanothus fendleri*

Field plots centered on aerial stem populations of *Ceanothus fendleri* were established in May, 1999, in three treated units (4, 5, and 10) of the Fort Valley Urban-Wildland Interface study site. Each of the three units were approximately 16 hectares in size and were thinned in late winter 1998-1999 according to overstory restoration guidelines. Sixty plots per unit were randomized into four experimental treatments (15 replicates per treatment per overstory unit). Treatments were combinations of protection from browsing and prescribed fire. Specifically, the treatments were as follows: 1) protection + no burning; 2) protection + spring fire; 3) no protection + no burning; and 4) no protection + spring fire. Plots were 2 x 2 m in size to capture most aerial stems in a clonal population. Measurement of these plots included all stems within a 56.4-cm radius (1 m<sup>2</sup>) from plot center. Steel rebar, pin flags, and metal tags marked plot centers. Ten additional plots, with no protection and no burning treatments planned, were established in each of three untreated, "control" units (3, 9, and 10b; see Fig. 1). These were used as a baseline for a "no action" management alternative.

## *Rosa woodsii*

In April 2000, six plots similar to those described for *Ceanothus fendleri* were established in each of six treated overstory units (1, 2, 4, 5, 7, and 10; see Fig. 1). The six treated units comprised two each of three replacement tree prescriptions designed as part of the larger restoration project mentioned above. Six plots also were established in each of two control units (3 and 9; see Fig. 1). Like *C. fendleri* plots, those used for *Rosa woodsii* plots were 1 m<sup>2</sup> in size (56.4 cm radius) centered on populations of aerial stems. Half of the plots were randomly selected for protection from large herbivores.

### Treatments

#### *Protection from Large Herbivores*

Large herbivore exclosures, 2 x 2 m in area, were constructed around selected *C. fendleri* and *R. woodsii* plots to protect plants from browsing animals. Exclosures were built of "rabbit wire" (~ 6 x 10 cm mesh) 1.2 m in height supported at four corners by steel T-posts. The small size of these plots discouraged deer and elk from jumping over the fencing and large mammal herbivory was effectively eliminated within exclosures.

#### *Prescribed Burning*

***C. fendleri*.** In order to burn selected plants, fire lines, 2 x 2 meters in size, were constructed around all *C. fendleri* plots in restoration units. Fire lines were continuous fuel breaks approximately 25-50 cm in width wherein all vegetation and forest floor material was removed exposing the mineral soil. Additionally, all downed woody debris larger than 5 cm in diameter was removed from plots in order to control fire behavior and severity on the plots.

*C. fendleri* plots were experimentally burned in April 2000 and May 2001 in coordination with United States Forest Service's (USFS) broadcast burning of the larger forest units. In April 2000, 24 *C. fendleri* plots (12 protected from herbivores, 12 unprotected) were burned in one of the restoration units. Drip-torches filled with a diesel-gasoline mixture were used to ignite forest floor material around edges of the plots and fires were allowed to burn until naturally extinguished. Due to extreme fire danger in spring 2000, the USFS halted all prescribed fires before we could complete treatments and no other plots were burned in this year. We were able to resume experimental burning in May 2001. At this time, sixty-five additional plots (33 protected, 32 unprotected) were burned in the two remaining restoration units.

Average and maximum flame lengths on plots were estimated during burning. To assess fire behavior, forest floor depth on plots was measured on *C. fendleri* plots within 2 months of burning following methods used at plot establishment. Additionally, burn severity for vegetation and substrate was categorized using a 5-class rating system (USDI 1992; e.g., 1 = most severe, 5 = unburned).

***R. woodsii*.** All *R. woodsii* plots were burned with the prescribed fires applied to the entire units by the United States Forest Service. Three units were burned in 2000 and the remaining three treated units were burned in 2001. No fire severity or behavior data were collected on burned *R. woodsii* plots.

### Vegetative and Reproductive Responses to Treatments

#### *Ceanothus fendleri*

Preliminary measurements of plots were conducted in May 1999. Measurements included number of aerial stems, average stem length, litter depth, and intensity of previous browsing (heavy, moderate, light). In June 1999 and 2000, all plots were examined for flowering stems. For all flowering stems observed, stem length and basal diameter were measured. Stems were classified into relative age groups and the number of inflorescences was counted. Groups used for age classification were based on stem appearance as follows: 1) class-one, or first-year stems, were not suberized, were generally supple, and had gray-green pubescence, 2) class-



2 stems were bright green and not suberized, showed lateral branches or indicated previous growth, and generally lacked pubescence, 3) class-3 stems were green but developing bark as evidenced by suberized patches, and 4) class-4 stems were dark brown-black and fully suberized.

In September 1999-2002, all plots were measured for population structure and annual production. All stems in plots were measured for length and basal diameter and stems were classified for age (described above). Average length of current-year branches was estimated and the longest current-year branch on each stem was measured. Number of current-year branches browsed on each stem was counted. Additionally, 50 current-year aerial stems of various sizes were collected from *Ceanothus* plants outside experimental treatment plots in 1999 and 45 were collected in 2000. These were measured for length and basal diameter. Stems collected in 1999 were oven dried at 70° C for 48 h and weighed to determine biomass and 1-sided leaf area of stems collected in 2000 was measured using a video projection system. These data were used to develop relationships that allowed estimation of current-year biomass and leaf area on *Ceanothus* plants within experimental plots.

*C. fendleri* seedling recruitment was assessed twice per year (July and September) and emerging seedlings were counted at each plot within the 2 x 2-m areas encompassed by fire lines and herbivore exclosures. Emergent seedlings were identified by their small stature (stem diameter < 0.5 mm, length < 5 cm) and the presence of cotyledons. Seedlings were mapped for relocation.

Overstory tree density was measured in 2001 at each plot using point sampling (Avery and Burkhart 1983). Wedge prisms of 20 basal area factor (BAF) were used for tree tallies. All tally trees were measured for diameter at breast height (1.37 m) and recorded in 4-cm diameter classes.

### *Rosa woodsii*

Preliminary measurements of *Rosa* plots were conducted in April 2000 and included stem number and average, tallest, and shortest stem height. Plots were remeasured in September 2001 to examine the effects of restoration treatments and browsing on plant growth and population characteristics.

### Sprouting Response of Cultured Rhizome Segments

Rhizomes and aerial stems of *Ceanothus fendleri* were collected monthly in 1999 to determine the effects of phenology and disturbance timing on sprouting potential and total nonstructural carbohydrate (TNC) patterns. Nine samples were collected from May through November 1999 in overstory units 4, 5, and 10 and in three untreated units. Understory communities were systematically searched for *Ceanothus* stems to be used for analysis. New areas of the units were searched every month to avoid sampling the same clones. When stems were found, notes regarding stem height and intensity of browsing were recorded. Rhizome connections were excavated and segments were removed just distal to aerial stems. Rhizome segment length was standardized to 20 cm for growth chamber incubation. Samples collected in the field were wrapped in moist paper towels, placed in plastic bags, and stored in a cooler with ice for transport to the laboratory. In the lab, rhizome segments were washed and dark-incubated at a constant 20° C in trays of moistened vermiculite for six weeks. At the end of the incubation period, rhizomes were removed from the growth chamber and measured. Rhizome segment diameter at both ends was measured. New shoots and activated buds were counted, measured for length.

In spring (May and June) 2000, rhizomes of *Ceanothus* and *Rosa* were collected, processed and measured as described above. This allowed a comparison of sprouting characteristics between the two species. However, due to delay and limitations concerning prescribed burning activities and their effect on seasonal fire components of this research, monthly rhizome collections were discontinued. This allowed us to concentrate research on feasible studies of shrub response to operational fire and browsing currently underway on field plots.

### Reproductive Output and Seed Fate

The vegetative studies described above were expanded in 2000 to more fully examine reproductive output and factors that influence seed survival of *Ceanothus fendleri* and *Rosa woodsii* growing under varying conditions. Methods were designed to quantify seed input to soil seed banks. Pre- and post-dispersal seed



predation rates were assumed to be important processes affecting input. Seed output data in combination with vegetative sprout production were used to determine potential reproduction in restored units.

Stems on very few (1.1%) *Ceanothus* plots produced flowers in 1999. However, flowering stems occurred on many plots in 2000 (see Results). Fruits that developed were counted in August 2000 and the number of fruit per branch on each stem was recorded. Mesh bag seed traps were fitted around fruits to capture seeds as they dispersed (explosive dehiscence). Seed traps were collected in August and all seeds were examined in the laboratory to determine maturity, soundness, and rate of insect parasitism. Stage of seed parasitism was classified as “emerged” (parasites had emerged from seeds at time of examination) or “not emerged” (parasite larvae or pupae found inside seed at time of examination). Parasites emerging from seeds were collected and photographed and specimens were sent to the USDA Systematic Entomology Laboratory for identification.

*Ceanothus fendleri* seeds collected in August of 1999 and *Rosa woodsii* seeds collected in 2000 from plants growing in the general area of the study site were used in a study to test post-dispersal seed predation. Main research questions focused on: 1) the overall rate of post-dispersal seed predation for the two shrub species, 2) the effect of overstory stand condition (thinned, thinned and burned, or untreated) on seed predation, and 3) the effect of substrate (charred and unburned pine leaf litter) on predation rate.

The experiment was a completely randomized, 3 x 2 x 2 factorial design (stand condition x substrate x species, respectively). A 250-m transect was established in each of nine overstory units that had been either thinned (three units), thinned and burned by prescribed fire in April 2000 (three units), or had not been treated (three units). At 50-m intervals (five points) along transects, seed depots were established. Each seed depot comprised four Petri dishes each containing either *Ceanothus* or *Rosa* seed and charred or unburned pine litter substrate. Seed depots were placed on transects September 7 and collected September 14, 2000. At collection, Petri dishes were covered and brought to the laboratory for processing. Seeds remaining in dishes were sieved from substrate and counted to determine the number removed by seed predators.

*Ceanothus fendleri* seeds were collected in 2001 from plants growing in the general area of the study site. These were used to examine post-dispersal seed predation as done in 2000. *R. woodsii* seeds were not included in the 2001 study. Further, the study was limited to treatment units and controls used for the *C. fendleri* plot-based studies. As in 2000, one transect was established within each of the six overstory units (3 treated and three controls). Transects were 250 meters long with seed depots every 50 meters. Each seed depot comprised two Petri dishes each containing ten *C. fendleri* seeds on charred or unburned pine litter substrate. Additionally, two Petri dishes each with ten sunflower seeds on charred or unburned substrate were randomly assigned to seed depots on each transect. Addition of sunflower seeds was designed to indicate seed predator preference and activity (Chambers pers. comm.). Seed depots were installed October 2 and collected October 11. At collection, Petri dishes were covered and brought to the laboratory for processing. As described above, remaining seeds were counted to determine the number removed by seed predators.

### Seed Germination

*C. fendleri* capsules were collected in late August 2001 from the site described above. Capsules from at least five shrub patches were collected and stored in paper bags until processed. In the laboratory, seeds were separated from capsules by gently grinding in a mortar and pestle.

In this study, we tested effects of heating and cold stratification on seed germination. Seed samples (n = 10) were separated from the collection and randomly assigned to one treatment of a 6 (temperature) x 2 (cold stratification) factorial design. We replicated treatments three times. Temperatures for seed heating tests were the following: no heat, 50, 70, 90, 110, and 130 °C. Seeds were heated in shallow aluminum pans for 10 minutes in an electric drying oven. Seeds were then either cold-stratified or left unstratified. Stratified seeds were placed between moistened filter papers in Petri dishes and allowed to imbibe water at room temperature (~ 20° C) for 24 hours. Petri dishes were then sealed in black plastic and placed in a cooler at approximately 4° C for 60 days. Seeds were germinated on moistened filter paper in Petri dishes in a controlled incubation chamber (Percival Scientific Inc., model 1500). Day length and temperature in the chamber were set to 14 hours, and 30° C, respectively. Full-spectrum, fluorescent lighting was provided during day periods. Night length and temperature were 10 hours and 20° C, respectively. Seeds were examined approximately every two days until germination

was completed (about 24 days). Germination was defined as successful if radicals extended beyond the seed coat by at least 2 mm. We did not study seed germination of *R. woodsii*.

## Data Analysis

### Effects of Herbivory

One-way analysis of variance (ANOVA) was used to test for effects of protection on vegetative characteristics of *C. fendleri* (1999 and 2000) and *Rosa woodsii* plants (2000 and 2001). Overstory unit or block was included in the ANOVA model as a blocking factor. Paired t-tests were used to test ( $P < 0.10$ ) between-year differences in vegetative parameters within treatment (protected and unprotected) groups for *C. fendleri*. Data for individual stems (i.e., length, number of current-year branches, length of current-year branches, biomass and leaf area per stem) were averaged at the plot level and analyses were performed on these values. Additionally, *C. fendleri* stem diameter, current year biomass, and current-year leaf area were summed at the plot level and analyzed for treatment differences. Morphological characteristics of *C. fendleri* tested were stem height-diameter ratio and branchiness. Branchiness was calculated as the number of current-year branches divided by stem length. Data met distribution and variance assumptions for ANOVA tests and were not transformed. In April 2000, 24 plots were burned as part of our fire effects experiment. These plots were excluded from analysis in year 2000.

A Mantel-Haenszel test was used to compare ( $P < 0.05$ ) proportions of unprotected and protected *C. fendleri* plots on which flower-producing stems were observed. Mann-Whitney nonparametric tests were used to analyze ( $P < 0.05$ ) differences in stem (*R. woodsii* and *C. fendleri*) and current-year branch (*C. fendleri*) number between treatments.

### Rhizome Sprouting Responses

Analysis of variance was used to test main effects ( $p < 0.05$ ) of collection month (May-November, 1999) on production of sprouts from cultured *C. fendleri* rhizomes. Parameters tested were average sprout length, sum sprout length (sum produced within a given month), and number of sprouts produced.

Number and sum length of sprouts produced by rhizome cuttings of *R. woodsii* and *C. fendleri* collected in June and July, 2000, were compared graphically since variability in sprout production and low replication made statistical analysis inappropriate.

### Effects of Thinning and Burning

Linear regression was used to analyze relationships between *C. fendleri* growth variables and overstory density and browsing. In order to achieve equal samples sizes from treated and untreated units, and because plants in untreated units were neither burned nor protected from large herbivores, ten plots that had not been burned nor protected from large ungulate herbivores were randomly selected from each unit ( $N = 60$ ) for these analyses. This selection allowed us to examine relative effects of thinning and herbivory across a broad range of stand densities. Significance level selected for regressions was 0.05. Overstory tree density values were derived using Reineke's stand density index (SDI; Reineke 1933) and tree diameters from point samples. Browsing values were calculated as the number of current-year branches browsed divided by the total number of current-year branches counted on each plot. *C. fendleri* growth variables analyzed were stem number, current-year branch length (average and longest), current-year biomass, and current-year leaf area for each of the four years of the study. All *R. woodsii* plots in treated overstory units were burned and therefore we could not analyze effects of thinning alone.

Relationships between SDI and finite rate of change (FRC) for *C. fendleri* aerial stem density (number of 2002 stems  $\div$  number of 1999 stems) were tested ( $\alpha = 0.05$ ). Data were natural log-transformed when examination of residual plots indicated increasing variance with increasing estimated values.

One-way analysis of variance (ANOVA) was used to test for effects of prescribed burning on *C. fendleri* within restoration units (no plots were burned in untreated units). Since significant differences in stem number, size, and current year biomass and leaf area had developed between protected and unprotected plots by the time

they were burned, effects of burning were analyzed for these two groups separately. Further, effects of burning were separately analyzed for plots burned in 2000 and 2001. Plots used for burn year 2000 comparisons were from within the same overstory unit. In ANOVA tests for burn year 2001 plots, overstory unit was included as a blocking factor. *C. fendleri* response variables analyzed were stem number, FRC, current-year branch number and length (average and longest), current-year biomass, and current-year leaf area. Data were natural-log transformed when necessary to normalize data distributions and homogenize variances. Significance level for tests was 0.05.

Logistic regression was used to test for relationships between *C. fendleri* mortality (categorical) and flame length and amount (cm) of forest floor consumed in burning. Linear regression was used to analyze the relationship between seedling emergence and forest floor consumption.

*C. fendleri* (we found no *R. woodsii* seedlings – see Results) establishment was assessed by evaluating: (1) emergence, defined as the number of first-year seedlings counted on a plot. These typically comprised cotyledons and one or more true leaves; (2) one-year survival, defined as the number of seedlings counted for emergence divided by the number of seedlings remaining on the same plot after the next growing season multiplied by 100 (e.g., [emergence 2000/remaining 2001] \* 100); (3) two-year survival, defined as the number of seedlings counted for emergence divided by the number remaining on the same plot after two growing seasons multiplied by 100 (e.g., [emergence 2000/remaining 2002] \* 100). Two-year survival assessment only applied to plots in unit 4, which were burned in 2000.

### Reproductive Output and Seed Fate

Chi-squared tests were used to analyze distributions of *C. fendleri* (we found no fruiting *R. woodsii* stems – see Results) stem sizes versus sizes of all stems in the population (all stems on protected, unburned plots) (Devore and Peck 1986). Normality of stem size distributions was assessed using normal probability plots. Stem length data were separated into 5-cm classes (df = 12) and stem diameters were placed in 0.1-mm ( $\log_{10}$  transformed) classes (df = 12) for analysis. A 0.05 probability level was used to determine significant deviation from chi-squared critical values.

Linear regression was used to examine relationships between *C. fendleri* fruit and seed production in 2001 and stem length and diameter. Data were natural-log transformed when residual plots showed increasing variance with increasing values of the independent variable. Relationships were considered significant at a 0.05 probability.

Mann-Whitney nonparametric tests were used to test differences in number of seeds removed from charred forest floor and unburned pine litter substrates in the post-dispersal seed predation experiments. A 0.05 probability level was used for tests of statistical significance.

### Seed Germination

ANOVA was used to test for effects of cold stratification (2 levels) and temperature (6 levels) on *C. fendleri* seed germination. Seed germination values were square-root, arcsine-transformed and a probability level of 0.05 was used to determine significance of main effects. One-way ANOVA was used to test for main effects of temperature alone. Bonferroni post-hoc tests were used to compare mean differences between temperatures (Kuehl 1994).

## **Results**

### **Pretreatment Characteristics on Plots**

#### *Ceanothus fendleri*

No differences ( $p > 0.05$ ) existed between groups in stem size or stem number in spring 1999. Stem density in plots ranged from 1 to 45 stems/m<sup>2</sup> and height ranged from 2 to 27 cm. Average number of stems per plot was 5.1 and average stem height was 7.6 cm. Stems in nearly all plots had been previously browsed.

### Rosa woodsii

Aerial stem densities in *Rosa* plots ranged from 2 to 13 stems/m<sup>2</sup>. Average number of stems per plot was 6.6. Stem heights ranged from 8 to 43 cm. Average stem height was 16.5 cm. Many stems showed signs of insect infestation (stem galls) as well as ungulate browsing.

### **Ungulate Herbivore Effects on Size and Biomass**

#### Ceanothus fendleri

Overall, exclosures were effective at protecting plants from large ungulate herbivory. Just over 2% of current-year aerial stems on protected plots showed signs of herbivory and this appeared to be from invertebrates. However, 64% of current-year stems in unprotected plots had been browsed. Plants not protected increased stem length by about 67% the first year, growing from 7.7 to 12.9 cm on average. Plants within exclosures increased length by approximately 220% from 7.5 to 24.1 cm on average. In September 1999, stems inside exclosures were significantly larger and retained more current-year biomass and leaf area than unprotected stems (Table 1). Average length of current-year shoots inside exclosures (13.1 cm) was more than two times greater than that of unprotected plants (4.7 cm). These differences were reflected in estimates of current-year biomass (Table 1). No differences were found between protected and unprotected plots for number of stems per plot or number of current-year branches per stem.

Size and biomass patterns between protected and unprotected plots found in 1999 generally persisted in 2000 (Table 1). Individual lengths of current-year branches decreased from 1999 averages and reflected droughty growing conditions that occurred in 2000. Interestingly, several vegetative parameters such as total stem length, sum stem diameter, and current-year biomass decreased on unprotected plots but increased on protected plots from 1999-2000. The results suggest that response of *C. fendleri* to droughty conditions is mediated by large ungulate browsing.

#### Rosa woodsii

In 2000, no significant ( $p > 0.05$ ) differences were found between mean *R. woodsii* stem lengths on plots protected from large herbivores and plots that were not protected (Fig. 2). In 2001, stems on protected plots were significantly ( $p < 0.05$ ) taller than stems on unprotected plots (Fig. 2). On average, protected stems were more than 30% taller than unprotected stems.

In 2000, similar ( $p > 0.05$ ) numbers of *R. woodsii* stems were found on plots protected from large herbivores and those not protected (Fig. 2). In 2001, significant ( $p < 0.05$ ) differences in stem density were present between protected and not protected plots (Fig. 2). On average, just over 28% more stems were found on plots protected from large herbivores.

### **Ungulate Herbivore Effects on Flower Production**

#### Ceanothus fendleri

In June 1999, three months after exclosures were established, no difference in flower production was found between protected and unprotected *C. fendleri* plots. Stems produced flowers on just two plots of 180 total (protected and not protected) located in treated overstory units.

In June 2000, flowering stems were found in a significantly ( $p < 0.001$ ) greater proportion of protected plots (55%) than unprotected plots (8%). On average, 22% (SE = 3.6%) of stems on protected plots produced flowers whereas 0.8% (SE = 0.4%) of stems produced flowers on unprotected plots. In protected plots, up to 11 (maximum) stems produced flowers whereas no more than one stem flowered in any unprotected plot.

Stems (all pooled) that produced flowers tended to be large and apparently older individuals (Fig. 3). No stems less than 20 cm in length produced flowers and 85% of the flowering stems were greater than 30 cm in length. Similarly, 82% of the flowering stems were greater than 4 mm in diameter. No current-year stems

Table 1. Means (and standard errors) of *C. fendleri* vegetative characteristics on plots protected from large herbivores and on unprotected plots in 1999 and 2000.

Variable	1999				2000			
	Protected		Unprotected		Protected		Unprotected	
Stems								
Number	8.1	(1.0)	6.9	(0.6)	9.1	(1.2) *	5.4	(0.5)
Length (cm)	24.1	(0.8) ** <sup>1</sup>	12.9	(0.7)	25.9	(1.0) **	11.2	(0.8)
Diameter (mm)	3.5	(0.1) †	3.1	(0.1)	4.1	(0.2) *	3.5	(0.1)
Current-Year Branches								
Number	5.3	(0.3)	5.3	(0.3)	15.3	(1.5) **	7.1	(0.6)
Length (cm)	13.1	(0.4) **	4.7	(0.4)	5.8	(0.4) **	2.5	(0.2)
Longest (cm)	19.5	(0.6) **	7.7	(0.5)	9.7	(0.6) **	4.5	(0.4)
Biomass (g)	1.4	(0.1) **	0.3	(<0.1)	1.6	(0.5) **	0.2	(<0.1)
Leaf Area (cm <sup>2</sup> )	83.9	(6.3) **	33.5	(3.3)	129.7	(26.1) **	27.1	(3.2)
Plot								
Sum Diameter (mm m <sup>-2</sup> )	24.5	(3.0) *	18.5	(1.5)	30.4	(3.4) **	17.1	(1.5)
Sum Current-Year Biomass (g m <sup>-2</sup> )	8.1	(0.9) **	1.7	(0.2)	8.7	(1.7) **	0.7	(<0.1)
Sum Current-Year Leaf Area (cm <sup>2</sup> m <sup>-2</sup> )	492.0	(55.0) **	177.5	(16.3)	739.1	(95.1) **	109.5	(9.7)

<sup>1</sup> Symbols indicate significant difference between treatments within years († P < 0.10; \* P < 0.05; \*\* P < 0.01)

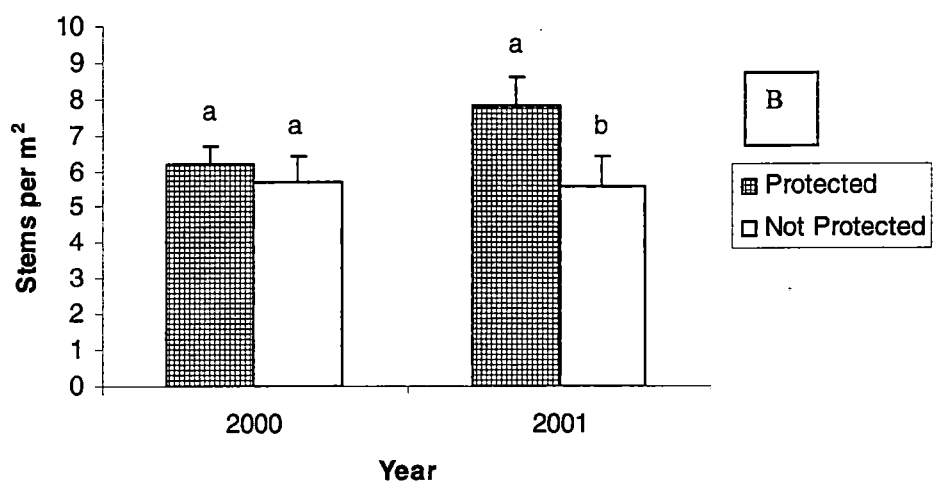
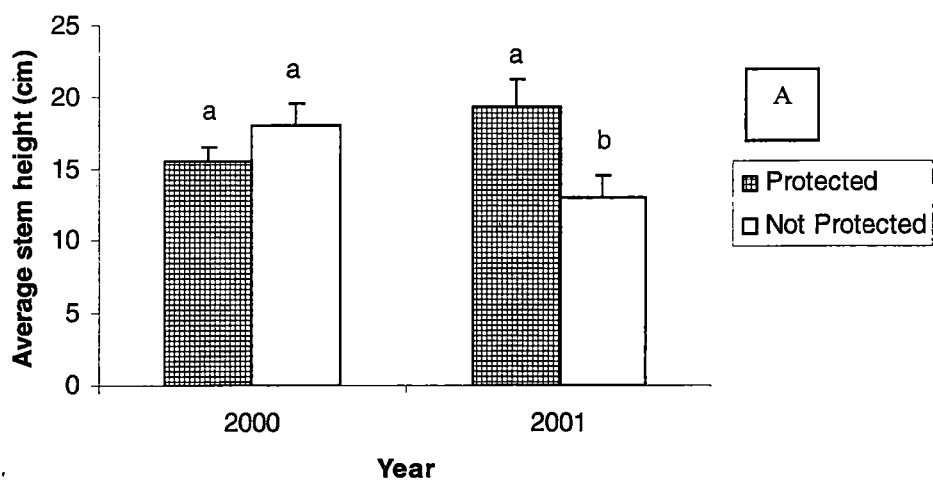


Figure 2. Stem height (A) and density (B) of *Rosa woodsii* on plots protected and not protected from large herbivores in 2000 and 2001.

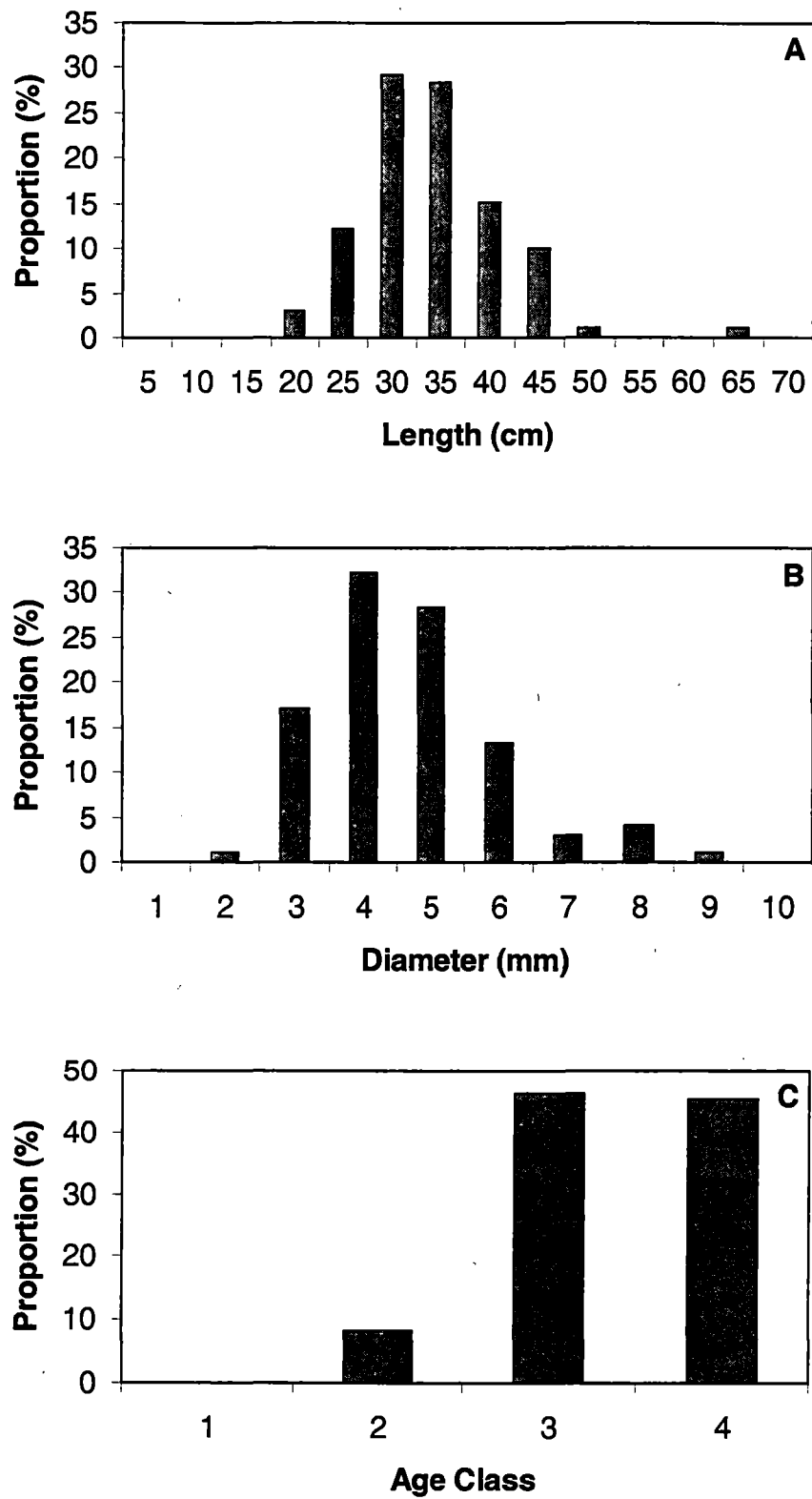


Figure 3. Proportion of *Ceanothus fendleri* stems that produced flowers by length (A), diameter (B), and age class (C).

flowered and more than 90% of the flowering stems were old enough to have suberized bases (age classes 3 and 4). The mean number of inflorescences (panicles) produced per flowering stem was 7.3. Inflorescences were comprised of many individual flowers although these were not counted. An average of two branches per stem flowered; the maximum number of flowering branches was nine per stem.

### *Rosa woodsii*

Neither flowers nor fruits were found on any *R. woodsii* stems in 2000 or 2001.

## **Rhizome Sprouting Potential**

### *Ceanothus fendleri* and *Rosa woodsii*

In 1999, *Ceanothus* plants in treated units began leaf expansion in early May. In late June, plants began stem elongation. Two plants in treated units were observed flowering. Plants remained in a stem elongation phenophase through August. By late September, plants appeared to enter fall dormancy. Due to the low number of reproductive stems in 1999, we were not able to identify fruit set, ripening, and seed dispersal phases (although see **Ovule and Seed Fate**).

Month of collection did not affect ( $p > 0.05$ ) sprout production of incubated *C. fendleri* rhizomes (Fig 4). Sum length, average length, and number of new shoots, were similar throughout the period of collection. For treated overstory units, there appeared to be a decrease in sprout production (sum length and number produced) during the months of July and August. This was a period of rapid stem elongation, likely associated with the onset of monsoon rains and increases in available soil moisture. This pattern was not apparent for stems in untreated overstory units (Fig. 4). Mean length of sprouts produced by incubated *C. fendleri* rhizomes across all collection months was 1.9 cm for both treated and untreated units. Average sum sprout length was 5.5 and 5.8 cm for treated and untreated units, respectively. Rhizomes from treated units produced an average of 2.9 sprouts across all collection months. Rhizomes from untreated units produced 3.0 sprouts on average.

Incubations of rhizomes in 2000 indicated significant ( $p < 0.05$ ) differences between *R. woodsii* and *C. fendleri* sprouting potential for rhizomes collected in the month of June. A greater number of sprouts were produced by *R. woodsii* than *C. fendleri* in both months (Fig. 5). Additionally, average sprout lengths of *R. woodsii* were longer than those of *C. fendleri*. Greater numbers of longer sprouts led to greater sum sprout length for *R. woodsii* compared with *C. fendleri* for rhizomes collected in June (Fig. 5). Sprouting potential of *C. fendleri* slightly increased in July, whereas that of *R. woodsii* slightly decreased. This led to no significant ( $p > 0.05$ ) differences between the two species for any parameters tested (Fig. 5).

## **Overstory Density, Herbivory, and Drought**

### *Ceanothus fendleri*

Values for SDI ranged from 124 to 1754 across all *C. fendleri* plots sampled. Significant ( $p < 0.05$ ) negative relationships were found between SDI and current-year branch lengths, biomass, and leaf area during 1999 and 2001 (Table 2). Similarly, sum current-year biomass and leaf area were significantly ( $p < 0.05$ ) related to SDI in all four years. Number of current-year branches produced on stems and number of stems per plot were significantly related to SDI in 2002. Finite rate of change for *C. fendleri* stem density was not significantly related to SDI. Although all variables tended to decrease with increasing overstory density, SDI alone explained a small fraction ( $r$ -squared up to 0.23) of the variation in the data. In 2000 and 2002, no significant relationships were found between SDI and branch lengths, average current-year biomass, or leaf area produced on individual stems.

Models that included browsing (percent of current-year branches browsed) as an independent variable increased  $r$ -squared to 0.47 (Table 3). Browsing alone was significantly ( $p < 0.05$ ) correlated with growth variables in 2000 and 2002 when SDI was not important. In 2002, browsing was not significantly related to *C.*



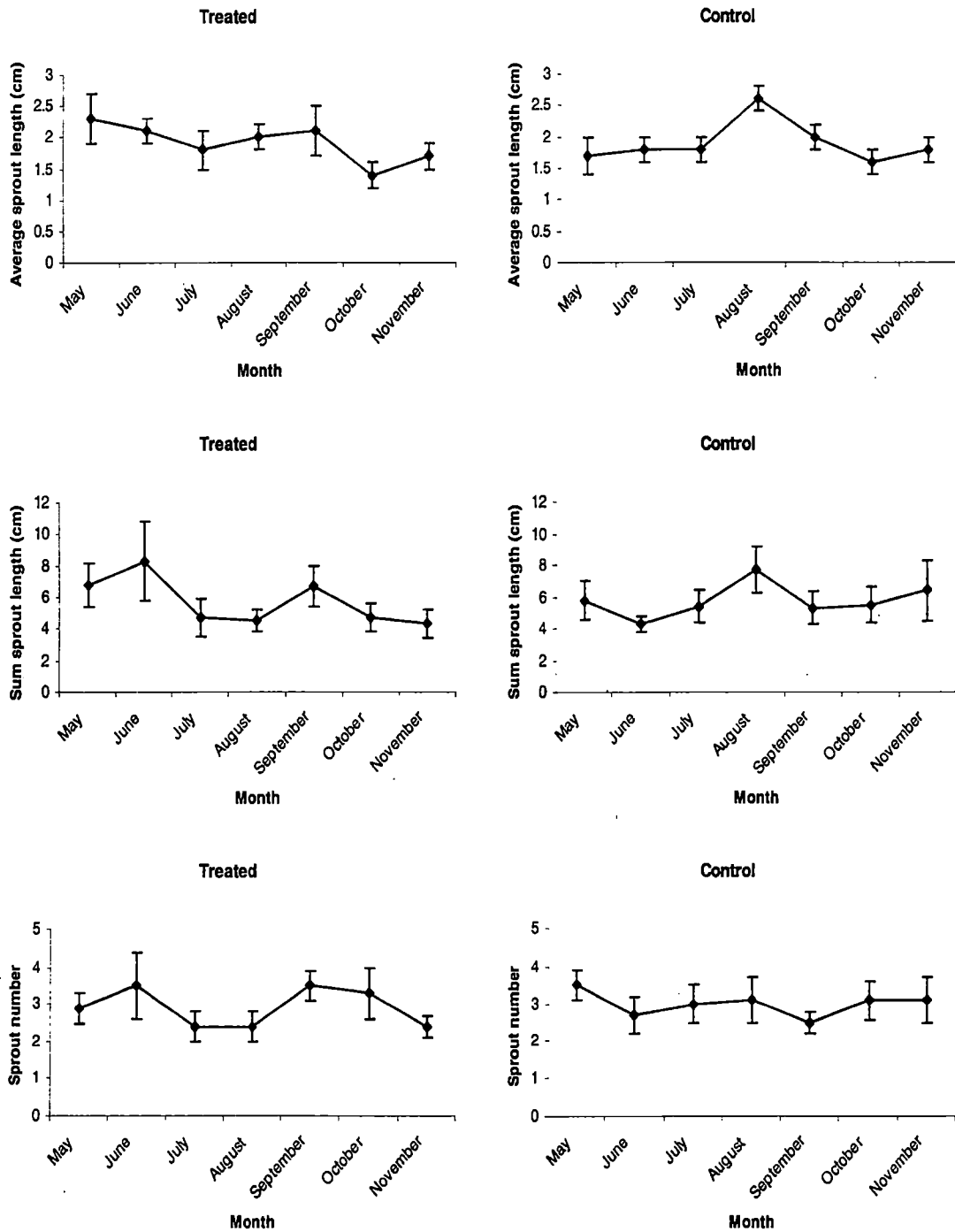


Figure 4. Average length, sum length, and number of sprouts produced on cultured *Ceanothus fendleri* rhizome cuttings collected from treated (thinned) and control (unthinned) overstory units May-November, 1999.

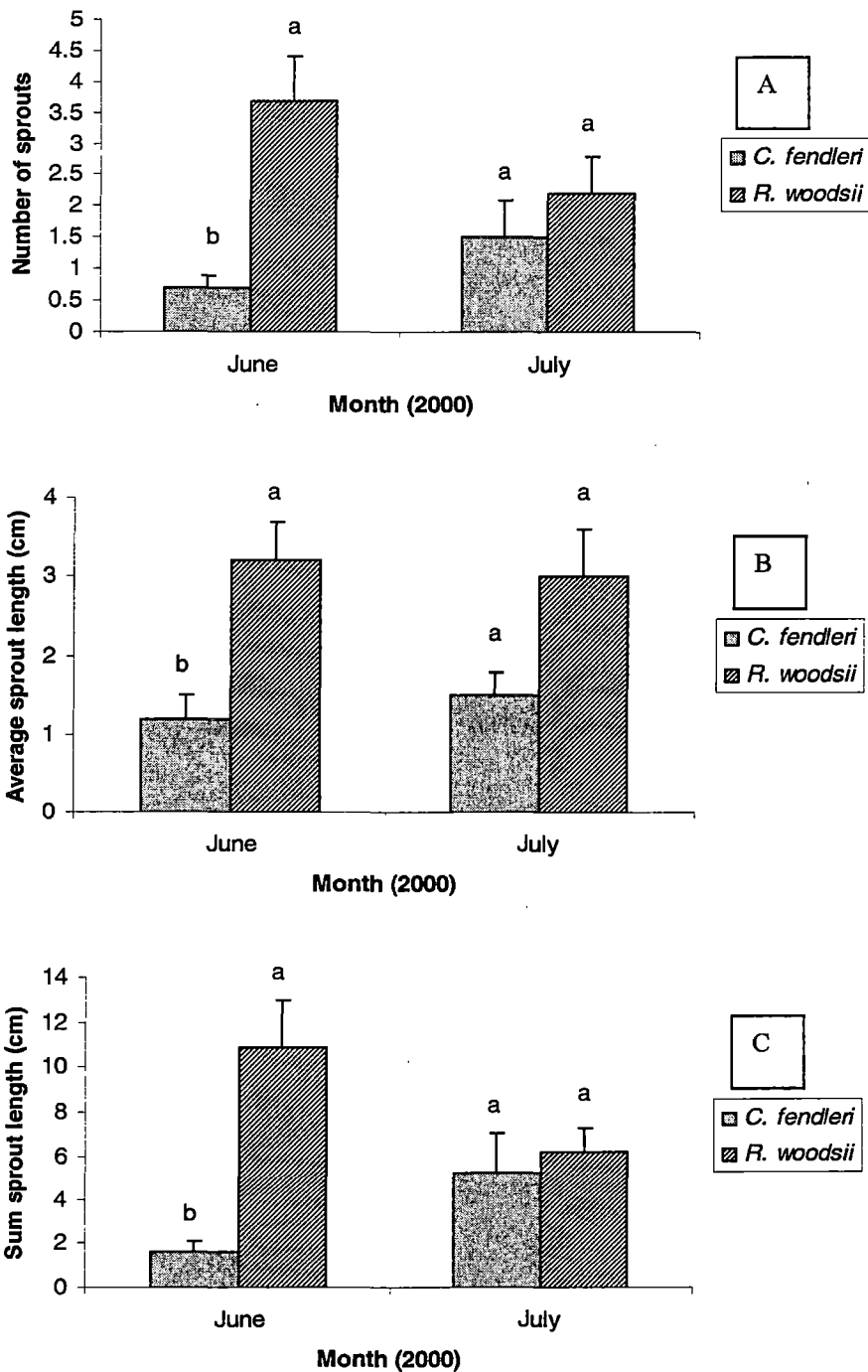


Figure 5. Comparison of number (A), average length (B), and sum length (C) of sprouts produced by cultured rhizome cuttings of *Ceanothus fendleri* and *Rosa woodsii* collected from the Fort Valley field site in June and July, 2000. Means for number of sprouts were determined for all cuttings including those which produced no sprouts (i.e., zero values included). Means for average and sum sprout length were determined only for cuttings that produced sprouts (i.e., zero values not included).

Table 2. Regression coefficients and P-values for models<sup>1</sup> of *Ceanothus fendleri* current-year growth as related to ponderosa pine stand density<sup>2</sup>.

Variable	Year											
	1999			2000			2001			2002		
	r <sup>2</sup>	r	P	r <sup>2</sup>	r	P	r <sup>2</sup>	r	P	r <sup>2</sup>	r	P
Mean branch length (cm)	0.08	-0.31	0.016	ns	ns	ns	0.23	-0.49	<0.001	ns	ns	ns
Longest branch (cm)	0.08	-0.32	0.014	ns	ns	ns	0.18	-0.44	<0.001	ns	ns	ns
Number of branches <sup>3</sup>	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.10	-0.34	0.013
Stem biomass (g)	0.10	-0.34	0.008	ns	ns	ns	0.10	-0.34	0.01	ns	ns	ns
Stem leaf area (cm <sup>2</sup> )	0.07	-0.29	0.026	ns	ns	ns	ns	ns	ns	ns	ns	ns
Plot biomass (g/m <sup>2</sup> )	0.21	-0.47	<0.001	0.06	-0.28	0.036	0.15	-0.40	0.002	0.12	-0.38	0.008
Plot leaf area (cm <sup>2</sup> /m <sup>2</sup> )	0.18	-0.44	<0.001	0.05	-0.27	0.046	0.10	-0.34	0.012	0.14	-0.40	0.005

<sup>1</sup>Models in the form:  $\text{Ln}(Y) = \beta_0 + \beta_1(X)$

<sup>2</sup>Reineke's (1933) stand density index

<sup>3</sup>Model in the form:  $\text{Sqrt}(Y) = \beta_0 + \beta_1(X)$

Table 3. Regression coefficients and *P*-values for models<sup>1</sup> of *Ceanothus fendleri* current-year growth as related to ponderosa pine stand density<sup>2</sup> and proportion of current-year branches browsed.

Variable	Year											
	1999			2000			2001			2002		
	<i>r</i> <sup>2</sup>	<i>r</i>	<i>P</i>	<i>r</i> <sup>2</sup>	<i>r</i>	<i>P</i>	<i>r</i> <sup>2</sup>	<i>r</i>	<i>P</i>	<i>r</i> <sup>2</sup>	<i>r</i>	<i>P</i>
Mean branch length (cm)	0.47	0.70	<0.001	0.11	-0.35	0.008	0.42	0.66	<0.001	ns	ns	ns
Longest branch (cm)	0.47	0.70	<0.001	ns	ns	ns	0.34	0.60	<0.001	ns	ns	ns
Number of branches <sup>3</sup>	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Stem biomass (g)	0.34	-0.34	<0.001	0.13	-0.38	0.003	0.24	-0.52	<0.001	ns	ns	ns
Stem leaf area (cm <sup>2</sup> )	0.19	0.46	0.001	0.08	-0.30	0.022	0.09	-0.32	0.020	ns	ns	ns
Plot biomass (g/m <sup>2</sup> )	0.27	0.55	<0.001	0.14	0.41	0.007	0.16	0.44	0.004	ns	ns	ns
Plot leaf area (cm <sup>2</sup> /m <sup>2</sup> )	0.18	0.46	0.001	0.09	0.35	0.030	0.09	0.35	0.036	ns	ns	ns

<sup>1</sup>Models in the form:  $\text{Ln}(Y) = \beta_0 + \beta_1(X_1) + \beta_2(X_2)$

<sup>2</sup>Reineke's (1933) stand density index

<sup>3</sup>Model in the form:  $\text{Sqrt}(Y) = \beta_0 + \beta_1(X_1) + \beta_2(X_2)$

*fendleri* branch length, current-year biomass or current-year leaf area, but did show a significant ( $p < 0.05$ ) negative correlation with number of stems per plot.

Annual precipitation played a significant role in determining the importance of overstory density and browsing on *C. fendleri* growth parameters. Although only four growing seasons were available to assess the relationship, a significant ( $p < 0.05$ ) positive trend was observed between correlation coefficients of *C. fendleri* growth models (current-year branch length response variable) and percent of average long-term precipitation for the months January-September (Fig. 6).

### *Rosa woodsii*

No significant ( $p > 0.05$ ) differences were found between vegetative characteristics of *R. woodsii* plants growing in untreated overstory units or those that were thinned for ecological restoration. Average stem height was not affected by overstory treatment in 2000 or 2001 (Fig. 7). Height averaged 15.5 and 18.0 cm on plots protected and not protected from large herbivores, respectively, in 2000. In 2001, stem height averaged 19.5 and 12.9 cm on protected and not protected plots, respectively.

Similar to stem heights, number of stems was not affected by overstory treatment in 2000 or 2001 (Fig. 8). Stem number on protected and not protected plots averaged 6.2 and 5.7 per m<sup>2</sup>, respectively, in 2000. In 2001, stem number averaged 7.8 and 5.9 per m<sup>2</sup>, respectively.

## **Experimental Burning**

### Burn Severity

In general, fire behavior and severity were similar on *C. fendleri* plots burned in 2000 and 2001 (Table 4). In 2000, burning resulted in mortality of 17% (4 of 24 burned) of *C. fendleri* plants. In 2001, 32% (21 of 65) of the burned plants died. For all burned plots combined, probability of mortality was significantly related to amount of forest floor consumed (Fig. 9). Probability of plant death increased dramatically after about 3 cm of forest floor consumption and no plants survived on plots where more than 6 cm of forest floor was consumed. Mean amount of forest floor consumption that resulted in mortality was 4.7 cm (SE = 0.4). *R. woodsii* plants died on two of 36 burned plots (no plants in control units died).

*C. fendleri* plants died on 6 of 37 (16%) plots for which vegetation burn severity was rated as "scorched" (vegetation burn severity class 4; USDI 1992). Depth of forest floor consumption on these plots averaged 1.3 cm (SE = 0.2). On plots for which vegetation burned severity was rated as "lightly burned" (vegetation burn severity class = 3), plants died on 12 plots (28%). On lightly burned plots, depth of forest floor consumption averaged 2.6 cm (SE = 0.3). *C. fendleri* plants died on 8 of 9 (89%) plots for which vegetation burn severity was rated as "moderately burned" or "heavily burned" (vegetation burn severity classes 2 and 1, respectively). On plots for which vegetation burn severity was rated as class 2, mean depth of forest floor consumption was 4.2 cm (SE = 0.7) and for severity class 1, consumption averaged 5.5 cm (SE = 0.5). Average and maximum flame lengths observed during experimental burning were not significantly related to *C. fendleri* mortality. Maximum flame lengths recorded were 91 and 117 cm on plots burned in 2000 and 2001, respectively. Mean flame length in the two burn years ranged from 13 to 19 cm.

### Vegetative Response to Burning

*C. fendleri* and *R. woodsii* resprouted from burned aerial stem bases or belowground structures within approximately 60 days of burning. Across all burned plots, 66-96% of *C. fendleri* aerial stems died back to ground level. The remainder resprouted from aerial stem bases. In general, burning converted *C. fendleri* and *R. woodsii* patches from all-aged stem assemblages to those dominated by first-year sprouts (Figs. 10, 11).

**Protected Plots.** Experimental burning did not significantly affect number of *C. fendleri* or *R. woodsii* stems on plots protected from large herbivores. Similarly, burning did not affect FRC for protected plots. Mean stem

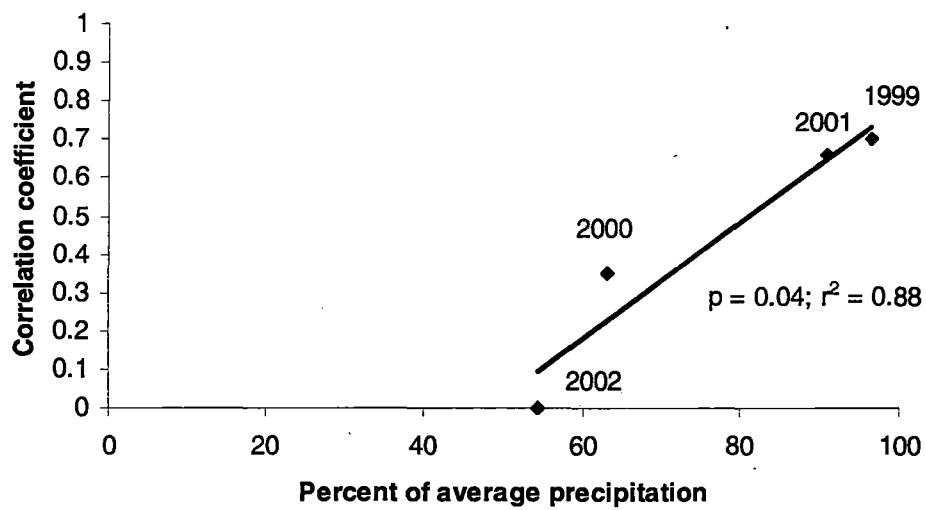


Figure 6. Relationship of *Ceanothus fendleri* growth model correlation coefficient and percent of average precipitation for months of January-September. Growth model is average current-year branch length as predicted by SDI (Reineke's stand density index) and percent of current-year branches browsed by large ungulates.

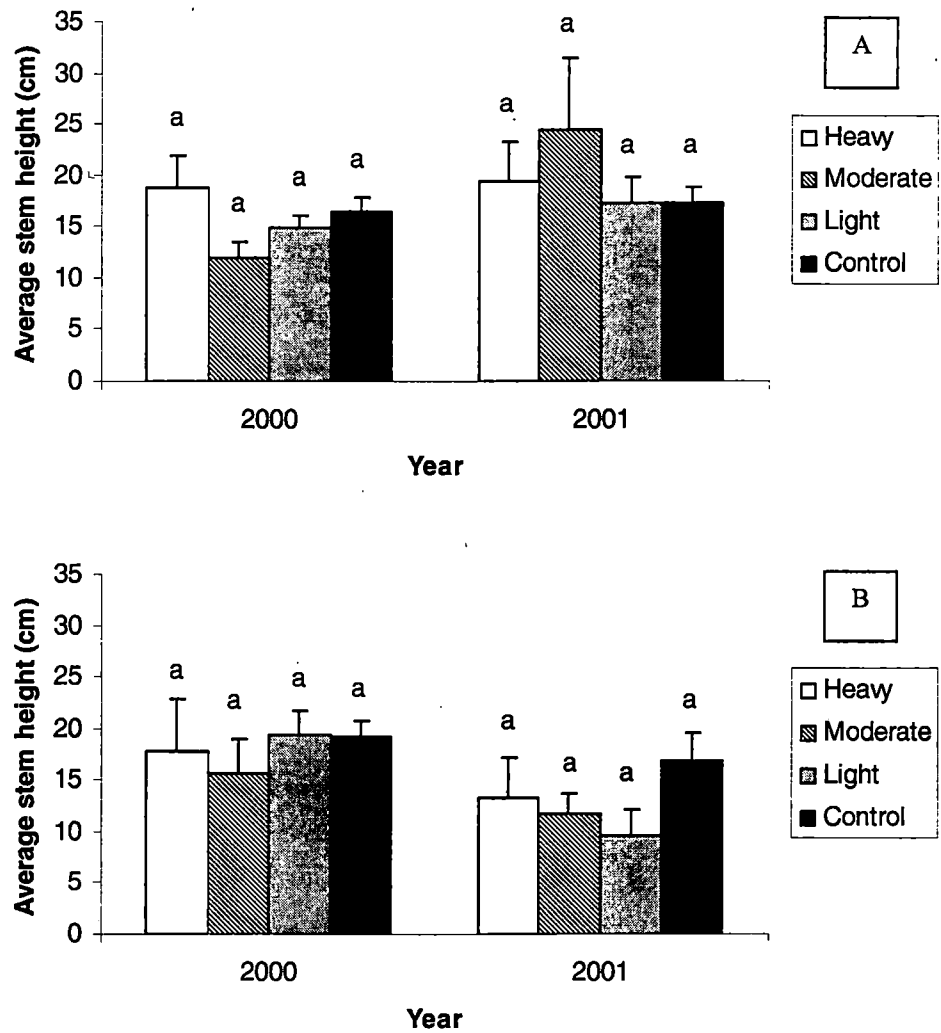


Figure 7. Average height of *Rosa woodsii* stems on plots protected (A) and not protected (B) from large herbivores in different restoration treatments. Treatments (Light, Moderate, and Heavy) refer to intensity of tree thinning in overstory units (see Study Area).

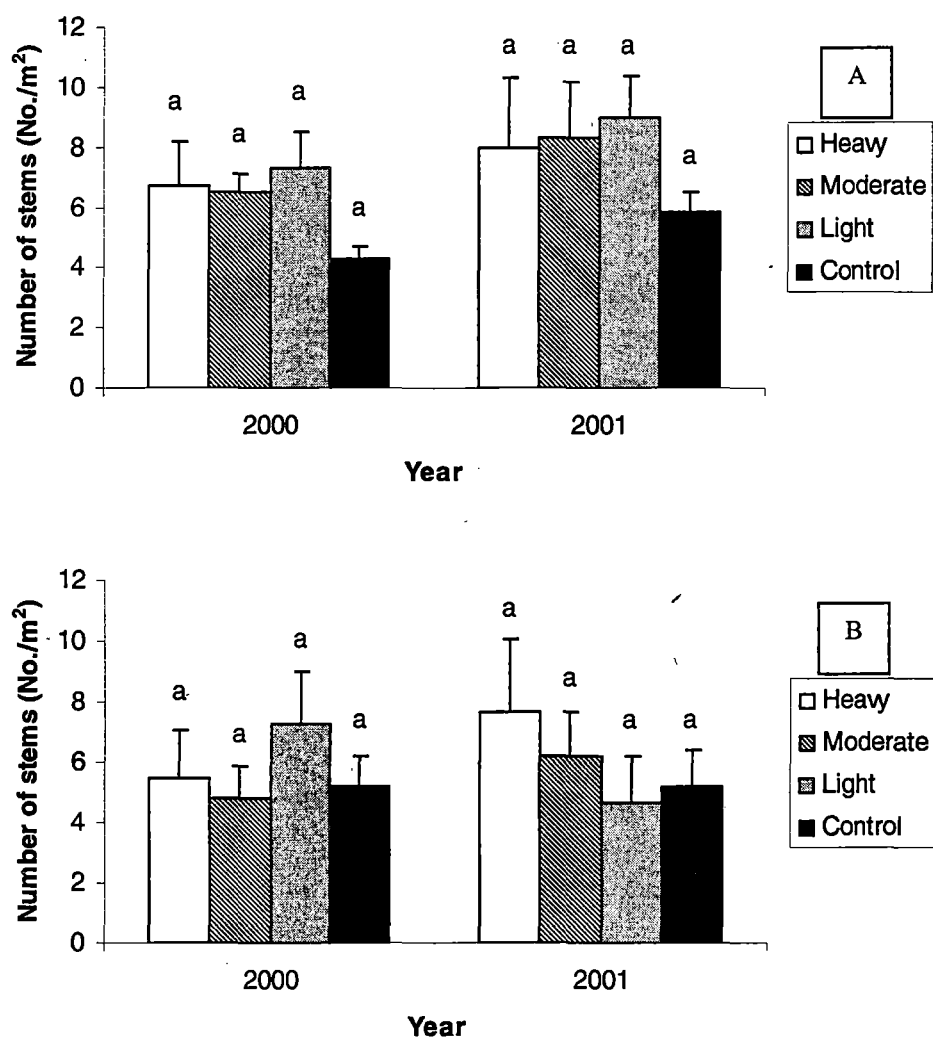


Figure 8. Number of *Rosa woodsii* stems on plots protected (A) and not protected (B) from large herbivores in different restoration treatments. Treatments (Light, Moderate, and Heavy) refer to intensity of tree thinning in overstory units (see Study Area).



Table 4. Means (and standard error) for fire behavior and severity variables on *Ceanothus fendleri* plots burned in 2000 and 2001.

Year	N	<u>Flame Length (cm)</u>		<u>Severity Rating</u>		<u>Forest Floor Consumption</u>	
		Average	Max	Substrate	Vegetation	Percent	Depth (cm)
2000	24	18.7 (1.5)	48.7 (5.7)	3.1 (0.1)	3.0 (0.1)	50.0 (5.7)	2.7 (0.4)
2001	65	12.6 (0.6)	36.8 (2.3)	3.2 (0.1)	3.3 (0.1)	52.0 (4.0)	2.3 (0.2)

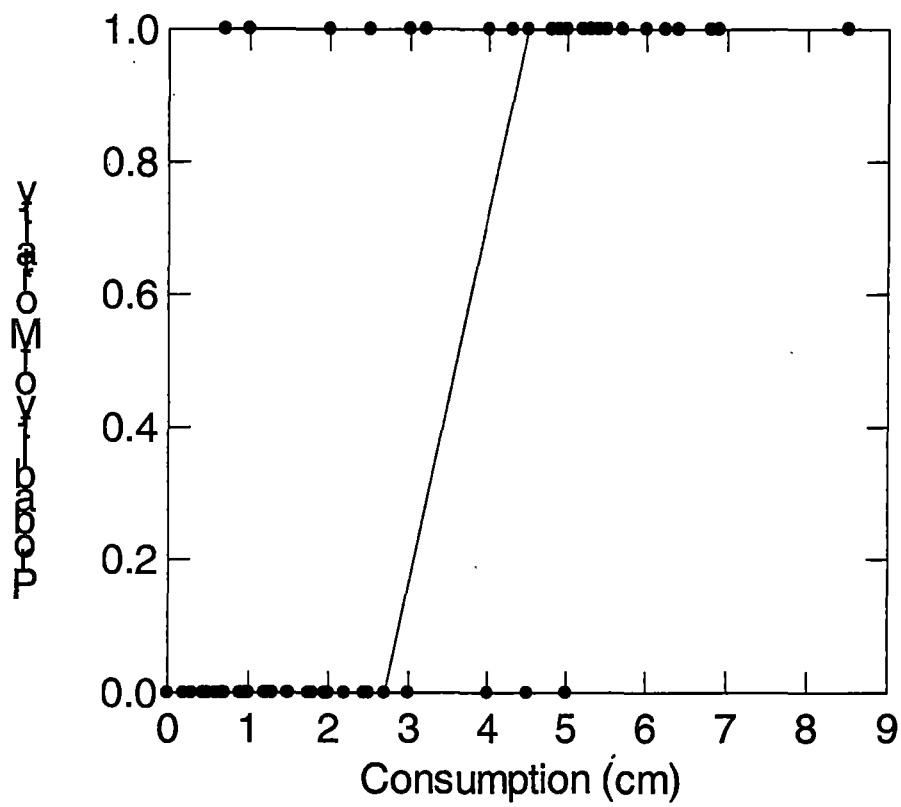


Figure 9. Probability of *Ceanothus fendleri* mortality as related to amount (cm) of forest floor consumed in experimental burns. Data are for plots burned in 2000 and 2001 pooled.

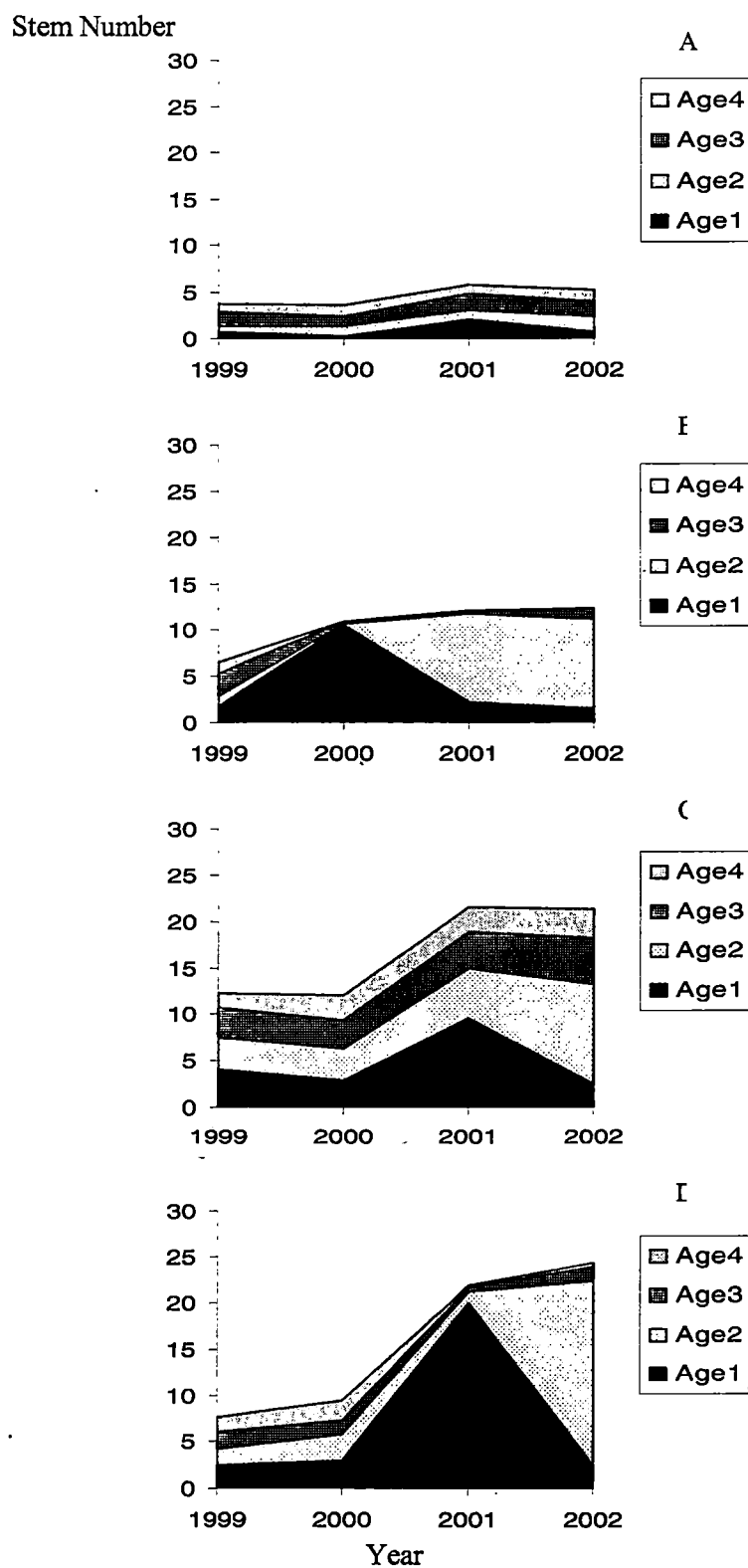


Figure 10. Distribution of *Ceanothus fendleri* stem age classes for plots protected from large herbivores. Plots not burned in overstory unit 4 (A) and burned in 2000 in unit 4 (B). Plots not burned in overstory units 5 and 10 (C) and burned in 2001 in units 5 and 10 (D).

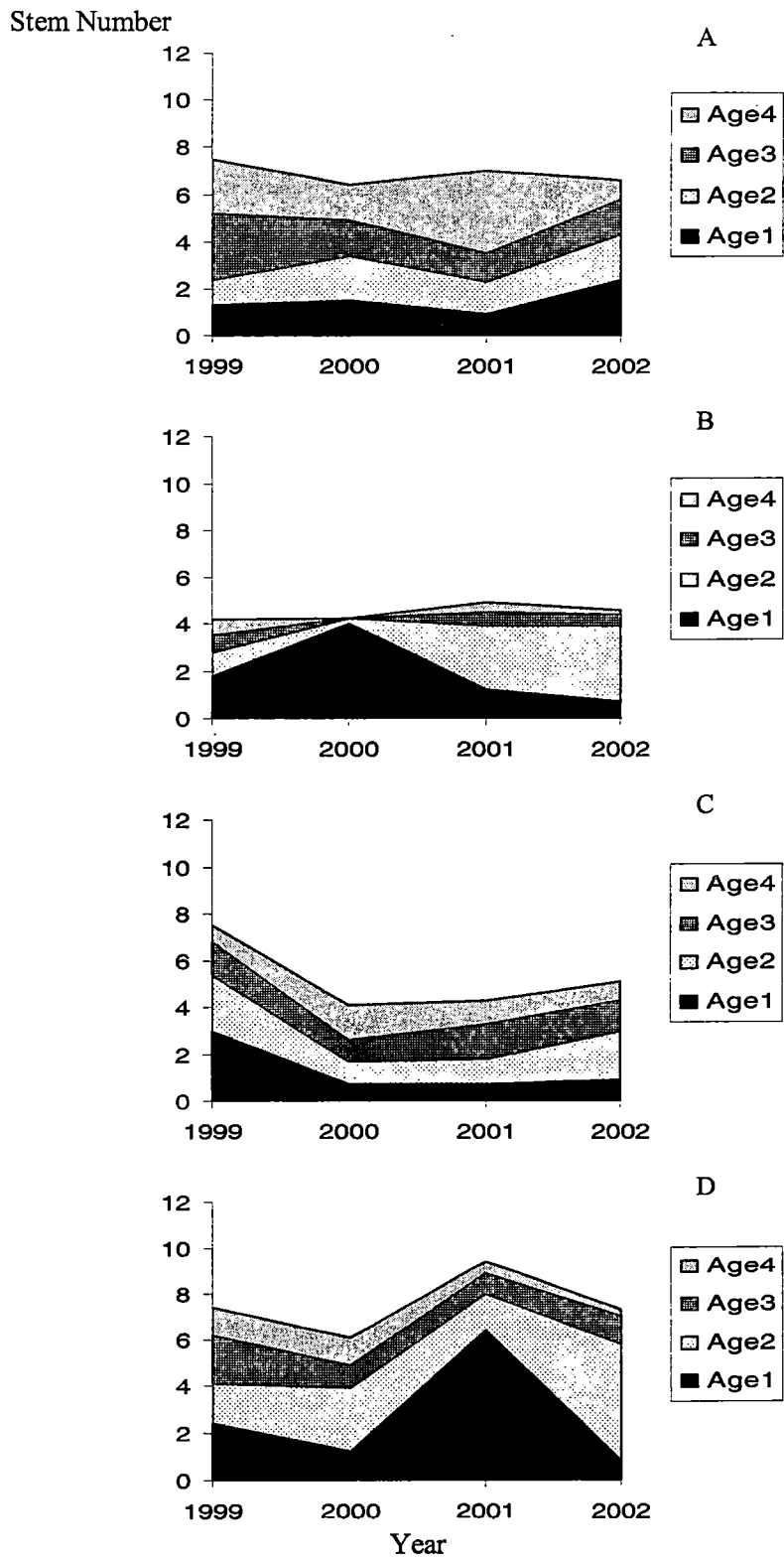


Figure 11. Distribution of *Ceanothus fendleri* stem age classes for plots not protected from large herbivores. Plots not burned in overstory unit 4 (A) and burned in 2000 in unit 4 (B). Plots not burned in overstory units 5 and 10 (C) and burned in 2001 in units 5 and 10 (D).

number generally increased on protected plots from 1999 to 2002 regardless of burning treatment and FRC ranged from 1.4 to 3.0 across burned and unburned plots (Fig. 10).

Burned *C. fendleri* plants produced longer current-year branches than unburned plants one growing season after treatment (Fig. 12). Current-year branches of burned plants were mainly sprouts originating from stem bases or belowground structures. These were long stems with relatively few lateral shoots. On protected plots burned in 2000, we measured current-year branches up to 43 cm in length.

Stems of unburned *C. fendleri* plants had significantly ( $p < 0.05$ ) more current-year branches than those of burned plants one growing season after burning (Fig. 12). For plots burned in 2000, differences in current-year branch number persisted for two growing seasons. More current-year branches on unburned plants translated to significantly ( $p < 0.05$ ) greater current-year biomass and leaf area than on burned plants (Fig. 11). No significant difference in current-year biomass was found between burned and unburned plants for those burned in 2000 (Fig. 12). Current-year leaf area was significantly ( $p < 0.05$ ) greater on unburned ( $95.8\text{--}138.0\text{ cm}^2$ ) stems than burned ( $40.1\text{--}59.4\text{ cm}^2$ ) stems one growing season after burning for both years (2000 and 2001 burns). In 2002, no significant differences were found between protected burned and unburned plots for any variable analyzed (Fig. 12).

*Unprotected Plots.* On plots that were not protected from large herbivores, *C. fendleri* stem number was significantly greater in 2000 (pre-burn;  $p < 0.05$ ) and 2001 (first-year post-burn;  $p < 0.01$ ) for plots burned in 2001 (Fig. 11). Although pretreatment (2000) differences were present, paired t-tests showed a significant ( $p < 0.05$ ) stem number increase on burned plots whereas stem number did not significantly change on unburned plots in 2001. Stem number was not significantly ( $p > 0.05$ ) different between unprotected burned and unburned plots in any of the four years for those burned in 2000 (Fig. 11). Similar to protected plots, FRC on unprotected plots was not affected ( $p > 0.05$ ) by burning and ranged from 1.2 to 1.4 across all unprotected burned and unburned plots.

One growing season after burning, mean current-year branch length was significantly greater on *C. fendleri* plants burned in 2000 than unburned (Fig. 13). In units burned in 2001, there were no significant differences in current-year branch length between burned and unburned plants (Fig. 13). Similar to protected plots, branch number on unprotected plots was greater on unburned plants than burned plants one growing season after burning for both burn years (Fig. 13). Pretreatment (1999) differences for current-year branch number existed for those burned in 2000, however, branch number significantly (Mann-Whitney test;  $p < 0.05$ ) decreased on these burned plots but did not significantly change on unburned plots one growing season after prescribed fire. Current-year *C. fendleri* biomass was significantly ( $p < 0.05$ ) greater on unburned stems than burned stems one growing season after burning for those burned in 2001 (Fig. 13). There was no current-year biomass difference between burned and unburned plants one growing season after burning for those burned in 2000. Current-year *C. fendleri* biomass was, however, significantly ( $p < 0.05$ ) greater on unburned stems in two growing seasons after burning (2001) (Fig. 13).

In 2002, no differences in current-year biomass were found for between burned and unburned plots for either burn year. Current-year leaf area on *C. fendleri* stems followed a similar pattern as biomass showing lower values on burned stems one growing season after burning with no differences between burned and unburned stems in 2002. Current-year leaf area on unprotected stems that were not burned ranged from 3.1 to 73.2  $\text{cm}^2$  across the four study years.

#### *C. fendleri* Seedling Establishment

No *C. fendleri* seedlings emerged on unburned plots in any of the four study years. On plots burned in 2000, seedlings emerged on nearly half (45.8%) the plots and a mean of 1.0 (SE = 0.3) per plot (2,500 seedlings per ha) were observed. Seedlings were found on 55% of plots burned in 2001 and emergence averaged 5.1 (SE = 1.4) seedlings per plot (12,750 per ha). The maximum seedling emergence occurred on a plot burned in 2002 where 53 seedlings (132,500 per ha) were observed. Protection from large herbivores did not significantly (Mann-Whitney;  $p > 0.05$ ) affect the number of seedling observed per plot for either burn year. Therefore, summaries for seedling emergence and survival are given for protected and unprotected plots combined.

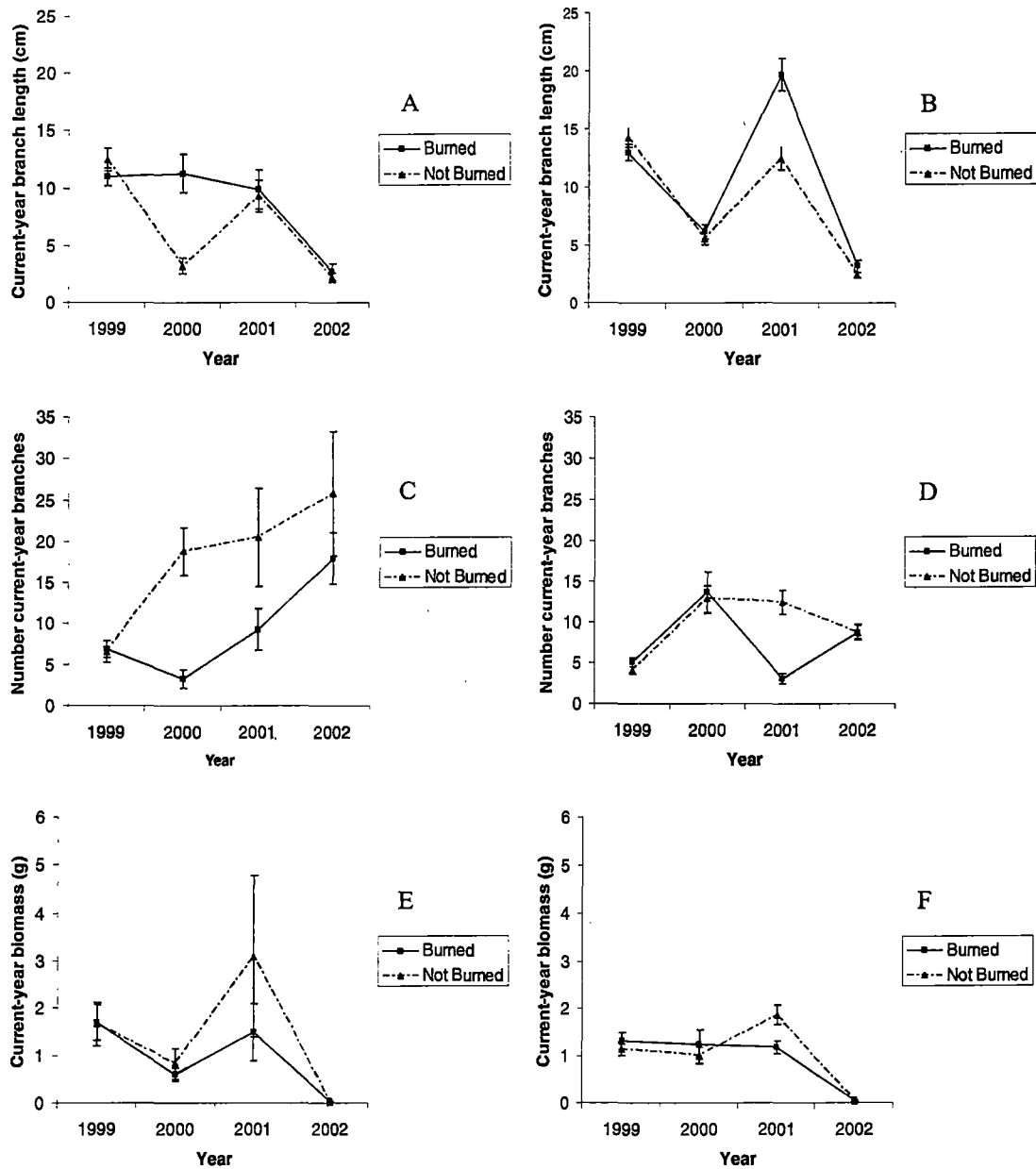


Figure 12. Average current-year branch length, number, and biomass of *Ceanothus fendleri* stems on plots **protected** from large herbivores. Plots in overstory unit 4 (A, C, E) were burned in 2000 and plots in units 5 and 10 (B, D, F) were burned in 2001.

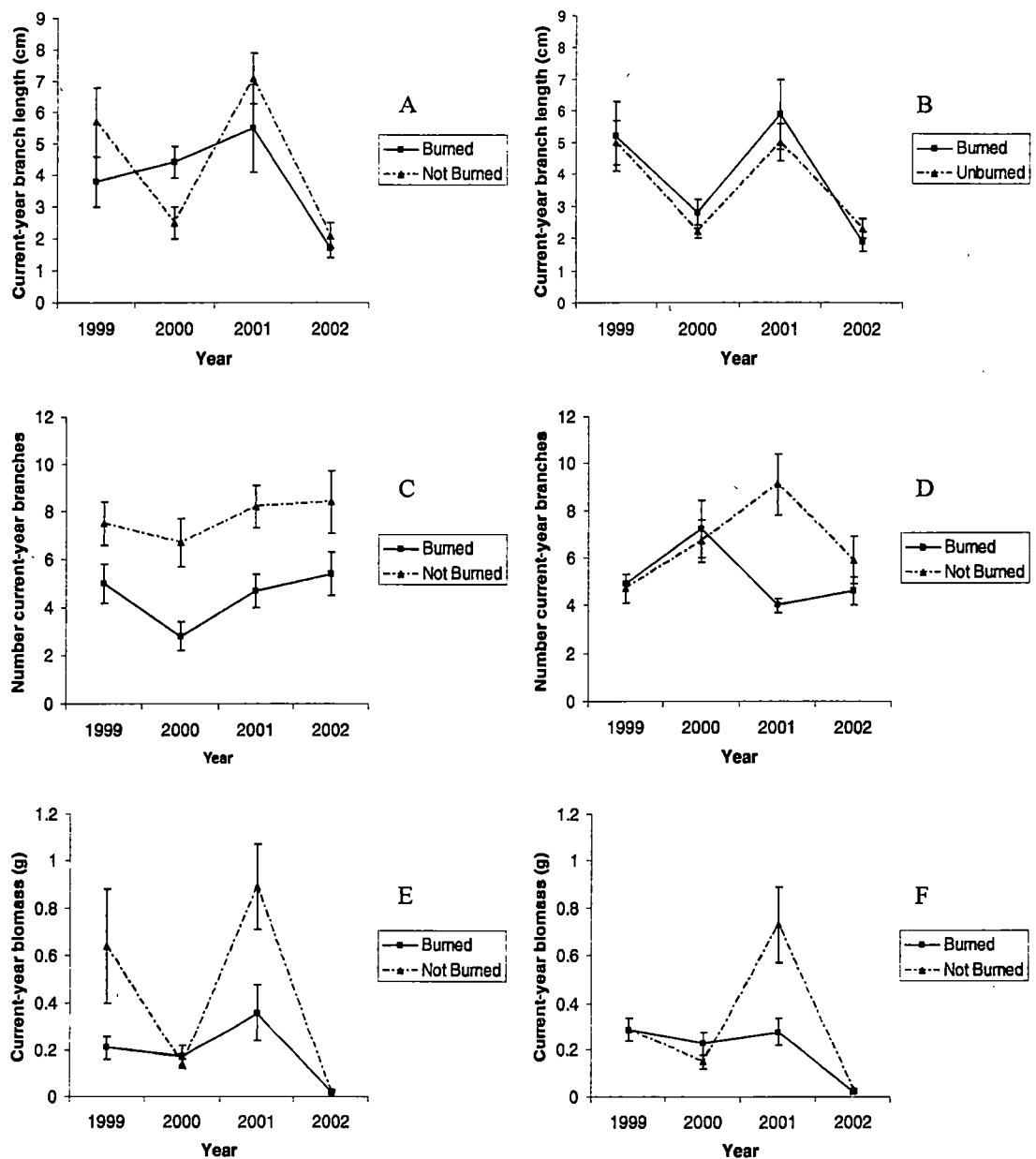


Figure 13. Average current-year branch length, number, and biomass of *Ceanothus fendleri* stems on plots **not protected** from large herbivores. Plots in overstory unit 4 (A, C, E) were burned in 2000 and plots in units 5 and 10 (B, D, F) were burned in 2001.

Number of *C. fendleri* seedlings emerging on plots was not significantly related to amount of forest floor consumed. However, a significant ( $p < 0.05$ ) relationship was found between probability of seedling emergence (proportion of plots on which seedlings emerged) and amount of forest floor consumed in 0.5-cm classes (Fig. 14). The form of the relationship was quadratic (i.e.,  $y_i = b_0 - b_1x_i^2 + b_{11}x_i$ ); seedlings were observed on a relatively small proportion (0 - 45%) of plots with either low ( $< 2$  cm) or high ( $> 7$  cm) amounts of forest floor consumed. Probability of emergence was greatest (45 - 100%) on plots with moderate (2.5 - 6.5 cm) amounts consumed.

Fire severity rating also corresponded to probability of *C. fendleri* emergence. Seedlings emerged on 18% (5 of 27) of plots rated as "scorched" (substrate burn severity class 4; USDI 1992). On these plots, mean depth of forest floor consumption was 0.8 cm (SE = 0.1). On plots rated as "lightly burned" (severity class 3), seedlings emerged on 66% (37 of 56) of plots. Mean amount of forest consumed on substrate burn severity class 3 plots was 2.5 cm (SE = 0.2). Seedlings emerged on 83% (5) of six plots rated as "moderately" or "heavily burned" (severity classes 2 and 1, respectively). On these plots, forest floor consumption averaged 5.6 cm (SE = 0.3).

One-year seedling survival was 26.7% (SE = 9.4) on plots burned in 2000. Live *C. fendleri* seedlings were found on 45% (5 of 11) of plots on which emergence was observed the previous year. Mean seedling density was 0.4 per plot (SE = 0.2) (1000 per ha).

One-year survival on plots burned in 2001 was 11.0% (SE = 4.7). *C. fendleri* seedlings were found on 55% (20 of 36) of the plots where they emerged and mean density was 0.5 per plot (SE 0.3) (1250 per ha). Mean first-year survival was not significantly ( $p > 0.05$ ) affected by protection from large herbivores for plots in either burn year. Two-year seedling survival on plots burned in 2000 was 3.6% (SE = 3.6). In 2002, two *C. fendleri* seedlings remained on just one plot. Average number of seedlings per plot was 0.08 (SE = 0.08) (200 per ha).

### Reestablishment of *R. woodsii*

Although sprout heights were similar between control and treated overstory units in 2000, stem populations in treated units were comprised mainly of new sprouts produced after burning. Thus, significantly ( $p < 0.05$ ) greater numbers of resprouts were present in treated versus control units (Table 5). As indicated by results of sprouting potential (see above), new stems were likely produced from rhizomes below ground. We saw no evidence of seedling establishment, nor did we find large storage organs such as lignotubers during excavations for sprouting potential experiments.

### **Ovule and Seed Fate**

Flowering of *C. fendleri* stems generally increases over the four study years (Fig. 15). In 1999, approximately three months after trees had been thinned, less than 0.05 stems per plot (one stem on 90 plots) were found with flowers (Fig. 15). In 2000, 99 stems across 78 plots flowered. In 2001, flowers were found on 238 stems across 62 plots and. Flowers were found on 276 stems across 78 plots in 2002 (Fig. 15).

In 1999, we observed empty *C. fendleri* receptacles on the single stem that had produced flowers earlier in the spring. It appeared that one or more fruit had been produced (0.01 fruiting stems per plot) (Fig. 15). In 2000, fruits were found on 14 stems across 78 plots in the three experimental restoration units (Fig. 15). From 1 to 28 fruits per stem were produced (mean = 7.4; SE = 3.2). This represented 3-84 potential seeds per stem, based on 3 possible seeds per fruit (Kearney and Peebles 1964). In 2001, *C. fendleri* fruit production increased dramatically and 172 stems (32 of 62 plots) were found with fruit (Fig. 15). From 1 to 408 fruits per stem were observed (mean = 39.4; SE = 7.4). This represented 3-1,224 potential seeds per stem. In 2002, we recorded complete failure of *C. fendleri* fruit production (Fig. 15). Although sample size was too small to statistically analyze, fruit production appeared to be related to winter plus growing season (Jan.-Sept.) precipitation (Fig.15).

Fruiting stem sizes (2001) were large relative to the total population of stems on plots (Fig. 16). Distributions of fruiting stem length and diameter were shifted towards the larger size classes in the population. No *C. fendleri* stems less than 20 cm in length produced fruit, although these sizes comprised approximately 15% of the total population. Similarly, no fruit was found on stems less than 3 mm basal diameter, although these stems comprised just over 28% of the total population.



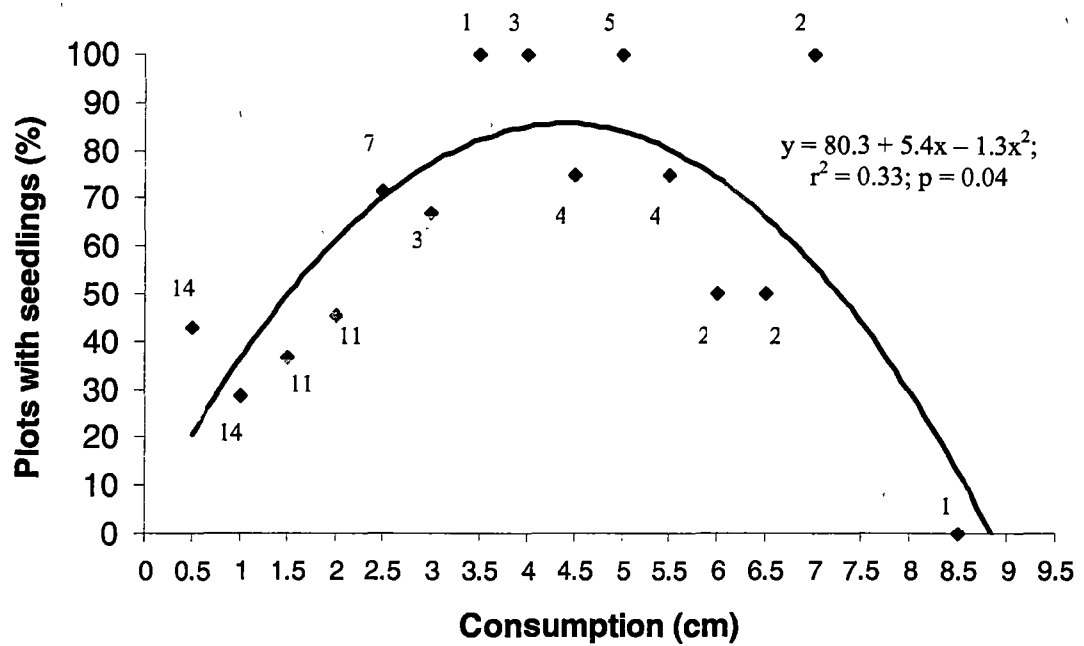


Figure 14. Relationship between proportion of plots on which *Ceanothus fendleri* seedlings emerged and forest floor consumption during experimental burning. Values shown in association with data points are number of plots in forest floor consumption classes.

Table 5: Mean number of new *Rosa woodsii* sprouts (No./m<sup>2</sup>) in different restoration treatments on plots protected and not protected from large herbivores. Treatments (Heavy, Moderate, and Light) indicate tree thinning intensity.

	Treatment				<i>Mean</i> <sup>1</sup>
	Heavy	Moderate	Light	Control	
Protected	7.7	7.8	7.5	1.3	6.0a
Not Protected	7.3	5.7	3.7	0.5	4.4a
<i>Mean</i> <sup>2</sup>	7.5a	6.7a	5.6a	0.9b	

<sup>1</sup> Similar lowercase letters in column represent similar means at  $p \geq 0.05$ .

<sup>2</sup> Similar lowercase letters in row represent similar means at  $p \geq 0.05$ .

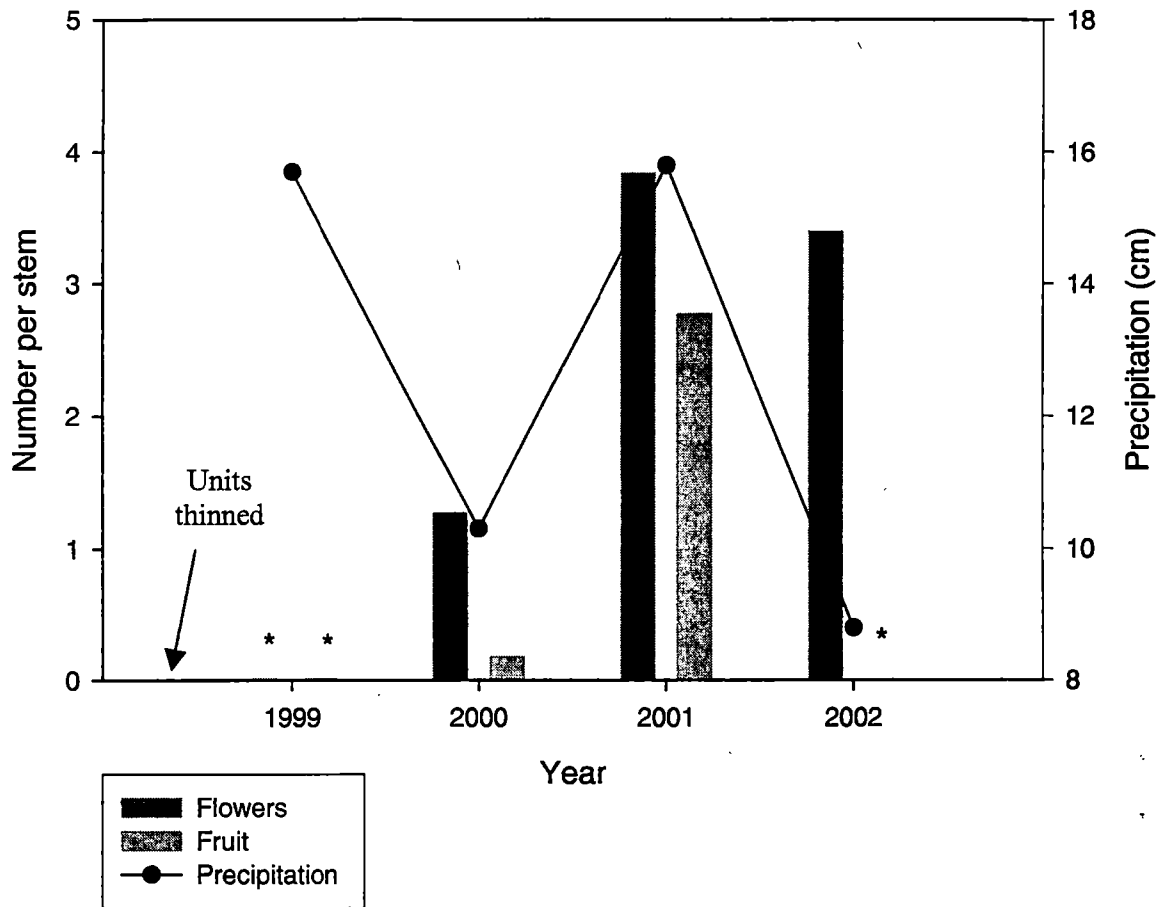


Figure 15. Number of fruiting and flowering *Ceanothus fendleri* stems per plot and precipitation (Jan.-Sept.) over four study years. Asterisks indicate less than 0.05 stems per plot.

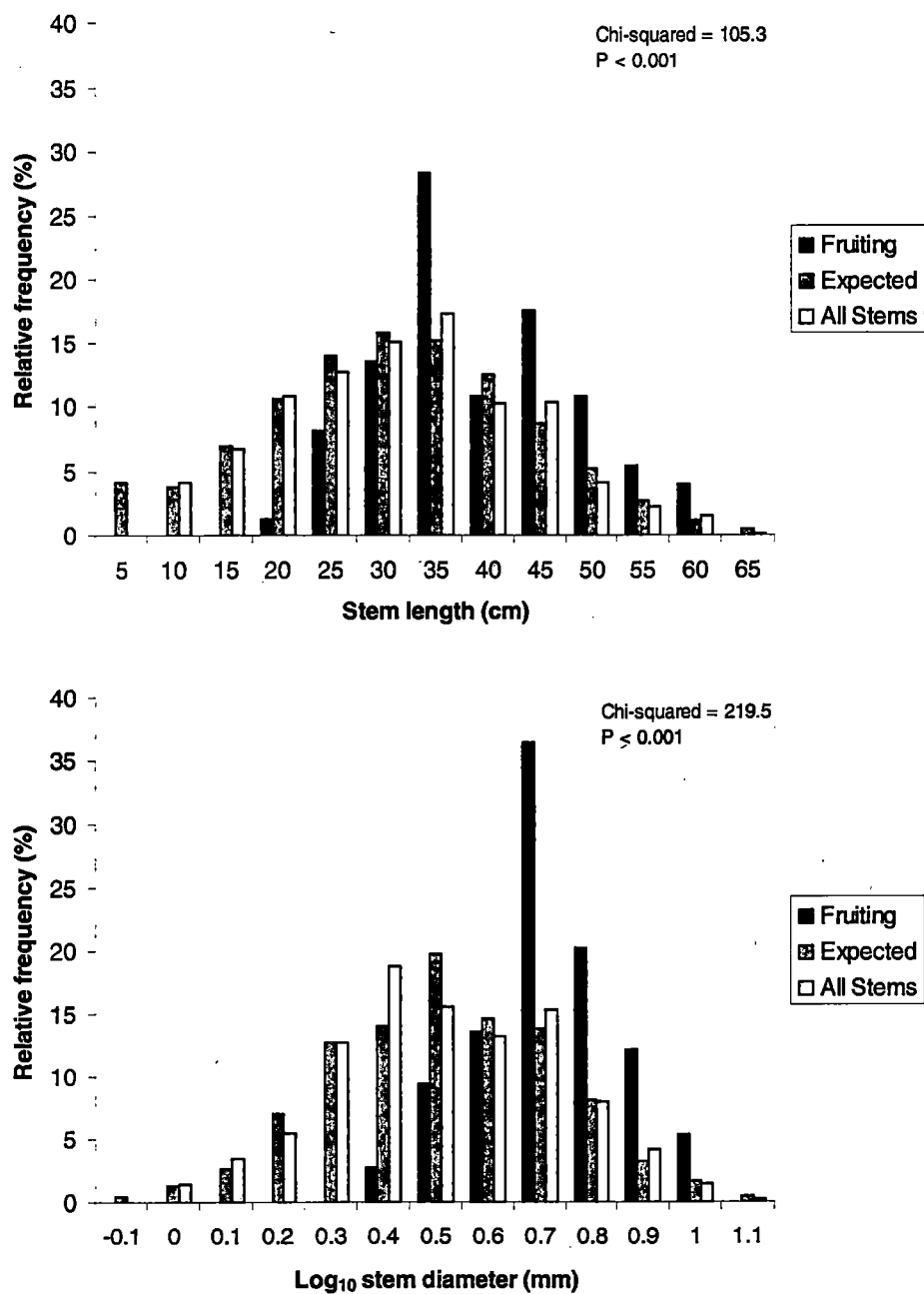


Figure 16. Comparison of *Ceanothus fendleri* fruiting stem length and diameter distributions versus expected values based on standard normal (z) curve areas. Normal curves constructed from means and standard deviations for all stems in *C. fendleri* population.

Although fruiting stems were relatively large, number of fruits produced per stem was not significantly ( $p > 0.05$ ) related to stem length. A weak positive relationship ( $r^2 = 0.06$ ;  $p = 0.02$ ) existed between *C. fendleri* fruit production and stem diameter.

Seed production patterns followed those found for fruiting. In 2000, seed-bearing *C. fendleri* stems produced 14.4 (SE = 7.8) total seeds on average. This represented a 35% ovule loss from the potential number of seeds (Fig. 17). Of the total seeds produced in 2000, 50.0% were undeveloped, 35.4% were parasitized by a chalcidoid wasp (Eurytomidae: *Eurytoma squamosa* Bugbee), 1.3% were hollow, and 13.2% were filled with apparently healthy embryos (Huffman 2002). Parasitized seeds housing immature wasps showed no visible signs of infestation. On average, 1.9 (SE = 1.6) sound seeds were produced per stem in 2000. This was equivalent to approximately 3,401 sound seeds per hectare.

In 2001, an average of 90.9 (SE = 26.8) total seeds per stem were produced. Similar to 2000 patterns, this number represented a 23% ovule loss from the potential seed number based on fruit production (Fig. 17). Undeveloped, parasitized, hollow, and filled seeds comprised 58.1, 3.1, 0.7, and 38.0%, respectively, of the total number produced in 2001. Number of sound *C. fendleri* seeds produced in 2001 averaged 35.0 per stem (SE = 11.8). Number of sound seeds per hectare in 2001 was approximately  $1.34 \times 10^6$ .

Similar to fruit production, linear regression analysis showed no significant ( $p > 0.05$ ) relationship between total number of seeds produced and stem length. A weak ( $r^2 = 0.09$ ;  $p = 0.005$ ) positive relationship was found between number of seeds produced per stem and stem diameter.

### Post-Dispersal Seed Predation

In 2000, few *C. fendleri* or *R. woodsii* seeds were removed from seed depots in any stand condition (control, thinned, thinned and burned). We found no significant ( $p > 0.05$ ) difference in counts of seeds removed from charred forest floor or unburned litter substrate (Table 6). Seed removal averaged 4.6.0% and 6.6% for *C. fendleri* and *R. woodsii*, respectively, across all samples.

Significantly ( $p < 0.05$ ) more *C. fendleri* seeds were removed from dishes containing charred forest floor substrate than those with unburned litter in 2001 (Table 6). On charred forest floor substrate, up to 70% of *C. fendleri* seeds were removed whereas maximum removal on unburned litter was 10%. Discarded *C. fendleri* seed coats at depots indicated that predators, probably rodents, immediately consumed seeds as they found them. Although too few samples made sunflower seed removal patterns difficult to assess, trends similar to those observed for *C. fendleri* were suggested. No sunflower seeds remained in charred forest floor dishes ( $n = 3$ ) whereas all 10 seeds remained in one dish ( $n = 3$ ; removal = 66.7%) containing unburned litter.

Accounting for post-dispersal losses in the three restored units where seed production data were collected, *C. fendleri* seed inputs to soil seed banks were approximately 3,333-3,401 and  $9.84 \times 10^5$ - $1.26 \times 10^6$  seeds per hectare for 2000 and 2001, respectively. Thus, overall ovule and seed losses from fruit production to seed dispersal across the four study years ranged from 71.2 to 100%.

### Seed Germination

No effect ( $p > 0.05$ ) of cold stratification on *C. fendleri* germination was found in the laboratory experiment. For cold-stratified and not stratified seeds combined, heat (10 minute duration) significantly ( $p < 0.05$ ) affected germination (Fig. 18). Seeds exposed to 90° C had higher germination rates than seeds receiving no heat, or those exposed to 50, 110, or 130° C. Temperatures of 90 and 70° C had a similar effect on germination. No seeds germinated after exposure to 130° C. Interestingly, exposure to 50° C reduced germination, although not significantly, compared with that of seeds which were not heated. *R. woodsii* did not produce fruit or seeds during the study period and no germination studies were conducted.

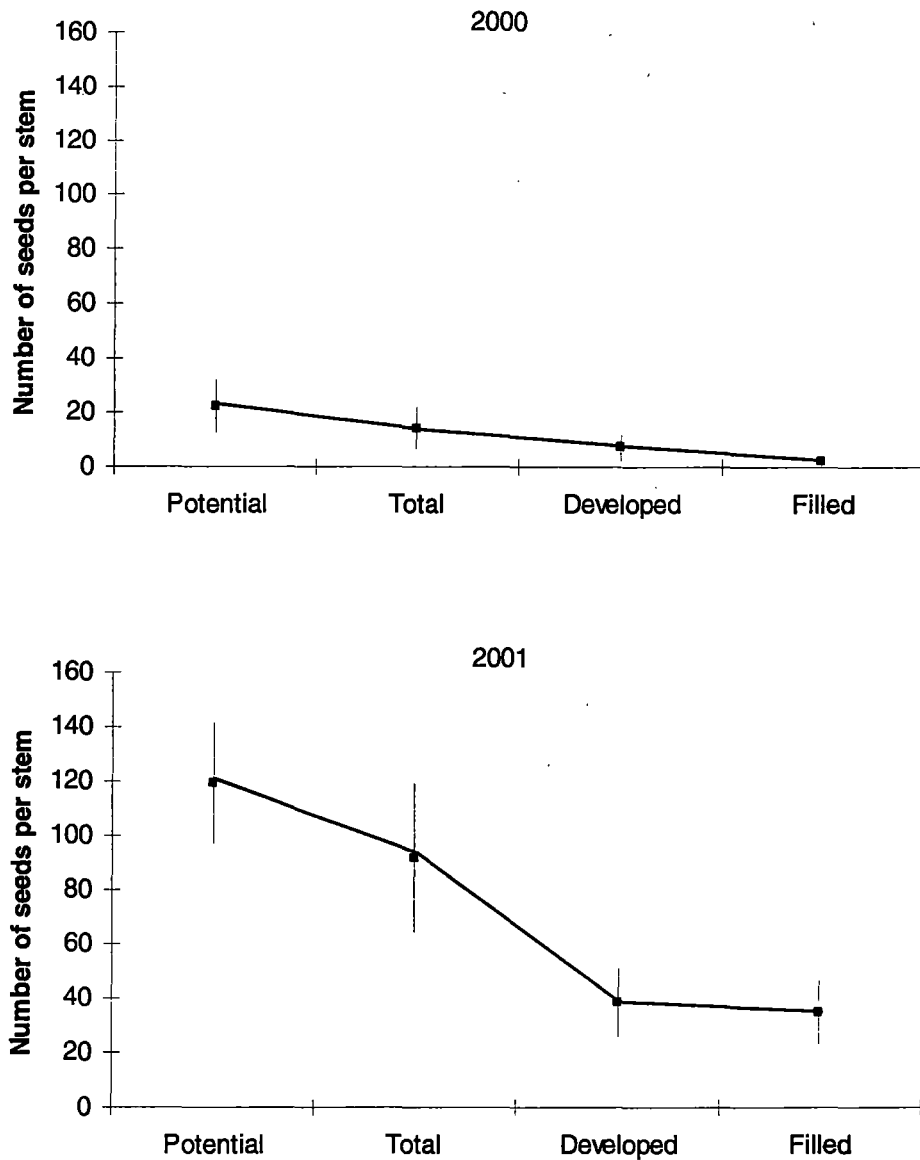


Figure 17. Number of *Ceanothus fendleri* seeds per stem in 2000 and 2001. "Potential" is estimated number of seeds in fruits enclosed by seed traps in July before dehiscence (3 seeds per fruit; Kearney and Peebles 1964). "Total" is number of seeds found in seed traps in August when collected. "Developed" is number of normal appearing seeds (~ 2 mm, dark brown, smooth seed coat). "Filled" is number of developed seeds with intact endosperm.

Table 6. Mean removal (%) of *C. fendleri*, *R. woodsii*, and *Helianthus* spp. seeds from charred forest floor and unburned ponderosa pine needles at seed depots in 2000 and 2001. Significant ( $p < 0.05$ ) difference in removal between charred forest floor and pine needles was found only for *C. fendleri* in 2001.

		2000						
Species	n	Control		Thinned		Thinned and Burned		Mean
		Charred	Litter	Charred	Litter	Charred	Litter	
<i>C. fendleri</i>	30	5.0	3.0	7.3	1.3	2.8	4.7	4.1
<i>R. woodsii</i>	30	8.9	4.2	9.3	1.3	6.0	6.7	6.1
		2001						
						Charred	Litter	Mean
<i>C. fendleri</i>	15	-	-	-	-	24.3	2.7	13.5
<i>Helianthus</i> spp.	3	-	-	-	-	100	66.7	83.3

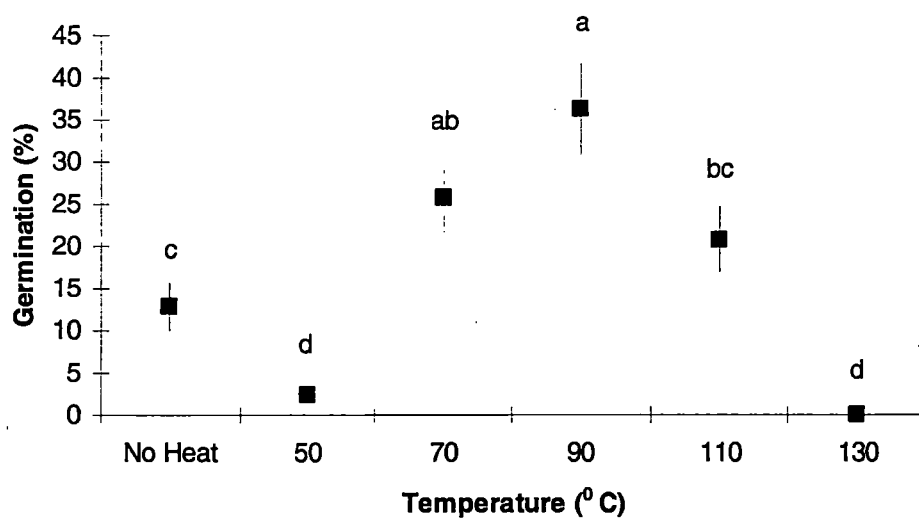


Figure 18. Effect of heat treatment on *Ceanothus fendleri* seed germination.



## Discussion

### Herbivory

Mule deer and Rocky Mountain elk appeared to be the primary large herbivores of *C. fendleri* and *R. woodsii*. These animals caused a significant reduction of current-year *C. fendleri* biomass in both study years. *R. woodsii* stems not protected from these herbivores were shorter than protected stems in all overstory conditions (i.e., treated and control). Further, fewer *R. woodsii* stems were found on plots open to browsers. Similarly, *C. fendleri* plants that were not protected from large herbivores had small, branchy stems, decreased aerial stem survival, and limited flowering compared with protected plants. Reduced flowering and stem survival could in turn lead to declines in local *C. fendleri* and *R. woodsii* abundance, affect community successional dynamics, and have indirect effects on other ecosystem components (Baines et al. 1994, Augustine and Frelich 1998).

It is clear that herbivory by deer and elk is limiting development of understory structure. Intensity of deer and elk herbivory on *C. fendleri*, *R. woodsii* and other species varies with season, site conditions, and ungulate population characteristics (Reynolds 1964, Patton 1974, Urness et al. 1975, Furniss et al. 1978, Allen 1996, Throop and Fay 1999). For example, Urness et al. (1975) found that *C. fendleri* comprised up to 6.9% of mule deer summer diet and was a consistently important browse species throughout the year at Beaver Creek, a site located around 55 km south of ours. Other woody species preferred by mule deer at Beaver Creek were Gambel oak (*Quercus gambelii* Nutt.), mountain mahogany (*Cercocarpus breviflorus* Gray), and Utah serviceberry (*Amelanchier utahensis* Koehne). These species are not commonly found on our study site and thus preference for *C. fendleri* may be greater at Fort Valley than that reported by Urness et al. (1975). Allen (1996) noted severe browsing of *C. fendleri* 15 years after an extensive wildfire in New Mexico and related intensity of herbivory to a dramatic elk population increase. Patton (1974) found that mule deer use increased in ponderosa pine forests after overstory thinning. Thus, deer and elk may have been attracted to the open conditions created by forest thinning treatments in our study.

Under conditions that stimulate flower production or enhance plant growth, herbivory may positively contribute to ecological restoration goals by providing resource richness and abundance for various organisms in the food web and enhancing ecosystem function (Jackson et al. 1995). Paige and Whitham (1987) reported increased flower production after experimental clipping as well as natural herbivory by deer and elk for a northern Arizona forb, scarlet gilia (*Ipomopsis aggregata* (Pursh) V. Grant). Similarly, Throop and Fay (1999) found that browsed New Jersey tea (*Ceanothus herbaceus* Raf. var. *pubescens* (T. & G.) Shinnery) produced a greater number of inflorescences than unbrowsed plants on a tallgrass prairie site. In contrast, Stein et al. (1992) noted that elk completely consumed arroyo willow (*Salix lasiolepis* Benth.) resprouts after experimental burning in northern Arizona. Similarly, Strohmeier and Maschinski (1996) reported both wild and domestic herbivores reduced total shoot length and number of branches of Arizona willow (*Salix arizonica* Dorn). Intense deer and elk herbivory can limit production of flowers, seeds, and vegetative regeneration of various plant species in other western ecosystems (DeByle 1985, Dunlap 1988, Mitchell and Freeman 1993, Hoffman and Wambolt 1996, Kay 1997, Opperman and Merenlender 2000). In our study, *C. fendleri* flowers were observed on less than 10% of the unprotected plots.

Further research is needed to explore the roles of wild ungulate herbivory in conservation and ecological restoration of Southwest ponderosa pine ecosystems. Current understanding of presettlement conditions – attributes that provide baselines to guide ecological restoration – is greatest for overstory characteristics and fire regimes (Covington and Moore 1994a, Covington et al. 1997, Fulé et al. 1997, Mast et al. 1999). Little is known regarding presettlement population dynamics and spatial distribution of large herbivores or the range of historical variability for their effects in Southwest forest ecosystems. On some landscapes, including that of our study area, elk are thought to be more abundant and distributed more evenly than they were for possibly the last 800 years (Allen 1996, Truett 1996, Kay 1997). Indeed, ungulate herbivory in combination with forest structural changes appears to be exacerbating conservation problems in these ecosystems. For ecological restoration activities that seek to reestablish ecosystem integrity and function, it is important to understand evolutionary environments of native species and emulate historical conditions of landscape-scale processes that include herbivory by large, wild ungulates.

## Sprouting Potential

Although we found no significant differences in *C. fendleri* sprout production between collection months throughout the growing season of 1999, a slight decrease in sum sprout length and number of sprouts was apparent in July and August, months of rapid growth. It is unknown whether this pattern will become more pronounced as *C. fendleri* over time due to release from overstory interference. A decrease in sprouting potential during phenophases of rapid growth is common for many plants. For example, fires during plant growing seasons have been reported to diminish resprouting potential and cause mortality in many species, particularly if burning is repeated annually (Lotti 1956, Ferguson 1957, Buckman 1964, Brender and Copper 1968, Young and Bailey 1975, Harrington 1985, Kauffman and Martin 1990). Ferguson (1957) concluded that, "the ability of a stem to sprout is probably a function of its physiological condition rather than the character of its injury". Kauffman and Martin (1990) reported that fuel consumption varied with season of burn and that shrub mortality patterns reflected fire intensity. However, they noted that shrubs appeared to be most resistance to fire-induced mortality prior to the initiation of aboveground growth and more susceptible during periods of rapid growth.

Although not tested in our study, stages of rapid growth often correspond to reduced levels of total nonstructural carbohydrates (TNC) in stem, root, and rhizome tissue. Low levels of TNS are often associated with reductions in sprout production potential (Trlica and Cook 1971, Menke and Trlica 1981, Harrington 1985, Hogg and Lieffers 1991, Zasada et al. 1994, Landhäusser and Lieffers 1997). Menke and Trlica (1981) suggested that the shape of the seasonal TNC cycle could indicate relative effects of defoliation on different plant species. For example, a narrow "V"-shaped pattern of seasonal TNC was associated with species that rapidly recovered carbohydrate reserves following defoliation. These species were least affected by defoliation compared with those showing broader "U"-shaped TNC patterns (i.e., longer periods with low reserves) (Menke and Trlica 1981). The pattern of resprouting we observed for *C. fendleri* appeared to be broad with low potential over two months (July and August). This may indicate a relatively lower ability to recover from disturbances occurring during these months. It should be noted that some *C. fendleri* plants sampled in our study had apparently been growing under dense stands of ponderosa pine for 30 or more years (Huffman unpublished data). Additionally, mechanical tree thinning in restoration units only months before our sampling undoubtedly affected the physiological condition of these individuals. Thus, resprouting potential exhibited by small rhizome segments excavated from remnant clones in this study was impressive.

## Importance of Overstory Density and Herbivory

Growth of *C. fendleri*, in terms of current-year branch length and number and current-year biomass and leaf area, was inversely related to overstory stand density and browsing. Height and number of *R. woodsii* stems were not affected by overstory condition in the two years reported here. Negative relationships between understory production and ponderosa pine overstory density have been reported by other authors (Arnold 1950, Ffolliott and Clary 1975, Bojorquez Tapia et al. 1990). Values of SDI in this study were within the range reported by Moore and Deiter (1992) who found a slight negative relationship between *C. fendleri* growth and overstory density in ponderosa pine forests of the North Kaibab National Forest in Arizona. In our study, browsing was generally more important than SDI in explaining variations in *C. fendleri* growth. For example, adding the proportion of current-year branches browsed to models explained 47% of the variation in 1999 current-year branch lengths whereas SDI alone explained just 8% (Tables 2 and 3). In other studies, shrubs have been found to weakly respond to changes in ponderosa pine forest density. For example, Moore and Deiter (1992) found that understory response was dependent on functional group (i.e., grass, forb, shrub, etc.) but it was not clear if this was due to factors related to plant physiological characteristics or extrinsic factors such as species interactions. The authors implied that domestic grazers were not present on their study site and elk were likely absent from their site on the North Kaibab National Forest (Moore pers. comm.). In a study of ponderosa pine stands in South Dakota, 6-8 shrub species were present yet only bearberry (*Arctostaphylos uva-ursi*), a species unavailable to browsers in winter due to snow cover, made significant contributions to production differences between overstory growing stock levels (Ursek and Severson 1989). Patton (1974) reported that grass and forb production, numbers

of browse plants (woody sprouts 30-137 cm in height), and large ungulate use all increased after harvesting ponderosa pine in patches 2-32 acres in size. We previously reported that *C. fendleri* plants protected from large herbivores retained nearly five times more current-year biomass than plants exposed to browsing by mule deer and elk (Huffman and Moore 1993). Allen (1996) speculated that severely browsed *C. fendleri* plants on a large wildfire site in New Mexico were the result of rapid post-fire increases in elk populations and elk use in the disturbed area. These results suggest that restoration thinning of dense forests has the potential to enhance growth of *C. fendleri* plants; however, response is constrained by large ungulate herbivory. Herbivore preferences and changes in use patterns can result in minimal benefit of changes in stand density for some understory species.

Climate affected the importance of relationships between *C. fendleri* growth, overstory stand density, and browsing. In drought years, models were insignificant or failed to explain more than 14% of the variation in the data (Table 2). A positive linear association between model correlation coefficients and percent of normal precipitation for important months substantiated these conclusions. Although our data was limited to just four study years, Fulé et al. (2002) suggested that droughty conditions in 2000 could have been, in part, responsible for no differences in understory cover between thinned and unthinned forests at Grand Canyon National Park.

### **Vegetative Response to Prescribed Fire**

More than one-fourth of all *C. fendleri* plants experimentally burned in this study did not resprout and mortality was related to amount of forest floor consumed. Although maximum flame length was never greater than 117 cm, which indicates relatively low fire intensity (Pyne et al. 1996), lethal temperatures belowground were apparently generated by smoldering combustion in deep forest floor layers. Significant (55-67%) *C. fendleri* mortality has been reported on similar sites when prescribed fire consumption of heavy (46.2-145.9 Mg/ha) forest floor fuel loads was high (55-95%) (Vose and White 1987, 1991). Smoldering combustion in duff layers is also responsible for mortality of presettlement-age ponderosa pine trees (Covington and Sackett 1984, 1992). Subsequently, land managers interested in forest restoration rake forest floor debris away from bases of presettlement trees before burning to reduce heat-related mortality (Fulé et al. 2001b, 2002). To reduce severe effects on the entire understory community, complete removal of the duff layer prior to initial reintroduction of surface fire has been tested (Covington et al. 1997). It is clear that initial reintroductions of fire in these ponderosa pine forests with deep forest floor fuel accumulations can be detrimental to remnant plant communities if burn conditions allow high rates of fuel consumption. Activities that result in mortality of existing plants -- individuals that can provide seed and cover for understory community development and soil retention-- are counter to ecosystem restoration goals.

*C. fendleri* and *R. woodsii* plants that survived prescribed fires resprouted readily and aerial stem populations were converted from all-age to even-age structures. Unburned populations remained all-age and stem number appeared to be stable over the four years of study. Annual recruitment of new *C. fendleri* stems in burned and unburned plots appeared to allow persistence by replacing stems lost to mortality. After two growing seasons, burned plants appeared to be regaining an all-age population structure. Sprouting and annual stem recruitment are important strategies for persistence in other competitive plant communities (Keeley 1977, Kurmis and Sucoff 1989, Huffman et al. 1994, Tappeiner et al. 2001). Keeley (1992) identified various vegetative strategies for shrubs after fires in chaparral including pulse recruitment of stems immediately after fire, continual turnover of stems through time similar to our findings for *C. fendleri*, and continual stem recruitment with little mortality. In general, sprout production after disturbance may be a viable strategy for persistence when safe sites for seedling regeneration are rare (Keeley 1977).

Persistence in understories may be further accomplished by production of long, unbranched sprouts after fire. Vigorous production of long sprouts may allow plants to quickly occupy growing space. Vose and White (1987) reported burned *C. fendleri* plants were similar in size to unburned plants one year after fire. In the present study, we found longer current-year branches on burned plants than unburned plants. Sprouts arising from belowground buds were up to 43 cm in length. Throop and Fay (1999), hypothesized that long sprouts produced by New Jersey Tea (*Ceanothus herbaceus*) after fire on tallgrass prairies may confer reproductive advantage stem size is often positively related to flowering. Indeed, we found that more than 80% of *C. fendleri* stems producing flowers were relatively large (> 30 cm length; > 4 mm diameter).

There were fewer current-year branches, less biomass, and less leaf area on burned plants than unburned plants but these differences were short-lived. Rapid recovery of *C. fendleri* to pre-burn size and production may allow this species to persist in understory communities that naturally burned at intervals less than 20 years before Euro-American settlement of the region.

### Regeneration from Buried Seed

Similar to plant survival, probability of *C. fendleri* seedling emergence was related to depth of forest floor consumed during experimental burns. Probability of emergence was greatest at moderate depths ( $2 > < 7$  cm) of consumption. Dormant *C. fendleri* seeds in soil seed banks were apparently stimulated to germinate after exposure to heat from fire (Story 1974, Krishnan 1989). Vose and White (1991) reported few *C. fendleri* seedlings on plots where fire intensities were low (open sawtimber), although they made no attempt to correlate fire behavior and emergence. A greater number of seedlings were found on plots with high fuel loads and heat yield (below canopy sawtimber and pole). Other *Ceanothus* species utilize a similar buried seed strategy and can form extensive brush fields on severely burned sites (Gratkowski 1974, Keeley 1977, Noste 1985, Conard et al. 1985, Keeley 1992).

We did not measure temperature profiles in forest floor and soils although our germination experiments indicated that temperature required to break seed coat dormancy and stimulate optimal germination is around 90° C. Many *Ceanothus* species require heat to allow opening of seed coats, although few show adverse response to heating (Hadley 1961, Quick and Quick 1961, Reed 1974). Story (1974) reported germination of *C. fendleri* seeds after treating with boiling water (100° C). Quick (1935) found temperature and cold stratification requirements varied for several *Ceanothus* species; some species showed negative responses to low ( $> 70^{\circ}$  C) levels of heat. Gratkowski (1974) found optimal temperatures for germination of mountain whitethorn (*Ceanothus cordulatus*) ranged between 90 and 105° C. Conard et al. (1985) generalized that temperatures greater than 120° C are lethal to *Ceanothus* seeds. These findings were corroborated by our germination studies. We found application of temperatures greater than 130° C caused seed mortality.

These results indicate that *C. fendleri* utilizes a dormant-seed regeneration strategy. This is a common trait of the *Ceanothus* genus in ecosystems ranging from coastal chaparral to ponderosa pine forests of the northwestern United States (Gratkowski 1974, Keeley 1977, Conard et al. 1985). A dormant-seed strategy is advantageous for recolonizing sites after severe disturbances such as infrequent fire. Temperatures in soil environments during fire vary greatly depending on fuel conditions, fire behavior, and depth in profile (Whelan 1995). Although *C. fendleri* has been reported to increase after prescribed burns and wildfires in ponderosa pine forests of the Southwest (Pearson et al. 1972, Ffolliott et al. 1977), few studies have documented germination of seedling emergence from seed banks (Vose and White 1987). In other ecosystems, *Ceanothus* seeds are thought to remain viable in soil for decades (Keeley 1977, Gratkowski 1974). Long-term seed viability of *C. fendleri* seeds is unclear although 40-year-old seeds can be successfully germinated (Huffman unpublished data). In contrast, our germination studies showed a fraction (20%) of seeds was able to germinate without being heated. These seeds may have short-term residence in seed banks. Findings of our studies suggest that *C. fendleri* strategies allow for recolonization of space immediately after disturbance (resprouting), seasonal colonization of new microsites (seeds without dormancy), and development of a dormant seed bank for colonization by new genets after more severe disturbances.

### Reproductive Capacity and Losses

Large differences in *C. fendleri* flower, fruit and seed production between the two study years (2000 and 2001) likely reflected combined influences of release from overstory competition and precipitation. For example, flower production generally increased for four years since time of overstory thinning in 1998-1999. This likely reflected improved microsite conditions. As described above (see Overstory Density, Herbivory, and Drought), negative relationships between vegetative production of understory plants and ponderosa pine overstory density have been widely reported (Ffolliott and Clary 1975, Ursek and Severson 1989, Bojorquez Tapia et al. 1990, Moore and Deiter 1992). Further, precipitation (Jan.-Sept.) in 2002, a year of abundant flower production but massive fruiting failure, was about 50% of the sites long-term average (Western Regional Climate Center 2003).

In 2001, precipitation was nearly equal (91%) to normal and both flower and fruit production were relatively high. Variability in fruit production has been linked to previous-year's precipitation for other species of *Ceanothus* in chaparral ecosystems (Keeley 1977, Keeley 1987, Zammit and Zedler 1992). Although, floral buds of these species are produced the year prior to flowering, our results suggest that widespread failure of fruit development can occur in extremely droughty years regardless of rates of flower production. In years of adequate precipitation, fruiting appears to be related to stem size. Although we found only a weak relationship between number of fruits produced and stem diameter, fruit production was observed on only the largest stems (both length and diameter) of the overall population. Similarly, Zammit and Zedler (1992) found that shrub size was the primary determinant of seed production for *C. greggii* plants that ranged from about 50-300 cm in height. Stem size hierarchies that lead to large intra-annual variation in seed production may not be present in our population. Further, these may not develop in *C. fendleri* populations that are frequently disturbed by burning.

Differences between potential and actual seed production indicated that about 1 ovule per fruit failed. Causes for ovule loss in this study are not known. In general, ovule losses are thought to be linked to lack of pollination, resource limitation, fruit abortion, and/or predation (Stephenson 1981). In 2001 and 2002, we observed flower visitation by various adult insects in the Lepidoptera and *Apidae* (Hymenoptera) (Huffman unpublished data); both groups are potential pollinators (Borror et al. 1989). Number and diversity of Lepidoptera have been found to increase after restoration treatments in ponderosa pine forests (Waltz 2001). We also observed species of *Cerambycidae*, insects that often feed on flowers and pollen (Huffman unpublished data). Furniss et al. (1978) speculated that psyllids may have contributed to ovules losses of redstem ceanothus (*Ceanothus sanguineus*).

Incomplete seed ripening was another consistently important (50-58% loss of total) source of seed loss in 2000 and 2001. Abnormal seeds with shriveled seed coats have been classified for other *Ceanothus* species as "unsound" (Furniss et al. 1978) and "aborted" (Zammit and Zedler 1992). Additionally, Keeley (1977) scored *Ceanothus* sp. seeds as "inviable" if embryos were shrunken or discolored as indicated by seed dissection. For redstem ceanothus, unsound seeds comprised 52-86% of the total crop over three years at three sites in Idaho (Furniss et al. 1978). Zammit and Zedler (1992) reported that 1.09-2.14 seeds per capsule were aborted for *C. greggii* over five study years; fewer seeds were aborted in stands of young (6-32 years) shrubs. Similarly, Keeley (1977) found that at least half the seeds produced by both *Ceanothus greggii* and *C. leucodermis* were not viable over three study years on a chaparral site in California. Causes for undeveloped seeds in our study are not known although other authors hypothesize that interactions of precipitation and plant carbohydrate stores determine seed outputs for *Ceanothus* species in chaparral (Keeley 1977, Zammit and Zedler 1992).

Predispersal parasitism was variably important (15-73% loss of developed seeds) in further reducing number of viable seeds. The chalcidoid wasp, *Eurytoma squamosa*, was the only predispersal seed parasite found. In an early note (Huffman 2002), we reported these findings to be an extension of the known range and host record for this insect. Parasitic wasps of the *Eurytoma* genus have been reported in seeds of several *Ceanothus* species and members of the *Rhamnaceae* family (Bugbee 1967, 1971, Furniss and Krebill 1972, Furniss et al. 1978, M. Gates pers. comm.). Little is known regarding the biology of these parasites or the interactions of their populations and *C. fendleri* seed production. Our data indicate that more than 2/3 of otherwise normally developed seeds can be consumed by this parasite in a given year.

Similar to seed parasitism, post-dispersal seed predation was a variably (2-24% of dispersed seeds) important source of seed loss. Although we did not attempt to determine identities of seed predators, discarded seed coats left at depots suggested that rodents were responsible for some predation. Rodents such as *Tamias cinericolis*, *Tamias dorsalis*, *Peromyscus maniculatus*, and *Neotoma* spp. are common in these forests and have been implicated in high (~80% removal) rates of seed predation in other studies (Compton unpublished data). In chaparral, harvester ants were found to be more important than nocturnal animals in removing *Ceanothus* seeds from experimental depots. Further, vertebrate predators were poor at locating seeds buried under plant litter (Mills and Kummerow 1989). Our results corroborate these findings and suggest that risks of predation are lowest when seeds disperse onto pine litter. Seeds rapidly percolate into this coarse substrate whereas on charred forest floor seeds are held on the substrate surface and exposed to predators.

## Conclusions and Management Implications

Our results indicate that tree reduction and prescribed fire treatments used to restore ecological function of ponderosa pine forest ecosystems have potential to increase *C. fendleri* growth and reproduction. No effects of overstory treatment were found for *Rosa woodsii*. Similarities among *R. woodsii* populations in treated and control units in 2001 suggest that this species can fully recover from prescribed fire in thinned forests within one year. Further monitoring is needed to determine long-term effects of overstory treatments on *R. woodsii*.

Large herbivores and drought limit *C. fendleri* and *R. woodsii* response to forest treatments. Protection of understories from deer and elk herbivory can allow plants to retain greater current-season production and accelerate understory development. Although our study did not address operational-scale herbivore protection, use of light logging slash (e.g., tree limbs and tops) to influence ungulate movement patterns and browse availability could be tested where desired or sensitive understory species are present. Further, assessment of the historic range of natural variability in elk numbers and spatial distribution would help managers formulate restoration objectives that include consideration of these wildlife species.

Effects of fire on demographic structure of *C. fendleri* populations depend on depth of forest floor consumed during burning. Preburn fuel measurements can be used to develop burn plans that encourage *C. fendleri* sprouting and seeding establishment and limit detrimental effects. Germination of *C. fendleri* seeds can be accomplished using heat treatments of temperatures between 70 and 90° C. Therefore, managers wishing to increase *C. fendleri* on sites can pre-treat seeds before sowing, or use low severity prescribed fire to stimulate natural seedling emergence (Vose and White 1987). Additionally, assessments of seed bank composition for these forests should include heating as a germination cue or otherwise risk underestimating *C. fendleri* abundance.

Although our studies did not examine effects of forest floor consumption on *R. woodsii* response, only two of 36 burned plants died after fire. The majority of plants we monitored resprouted vigorously from stem bases and belowground structures. Thus, both *C. fendleri* and *R. woodsii* are capable of sprout production following disturbance to aerial stems. Growth chamber studies suggested that *R. woodsii* was a more vigorous sprouter than *C. fendleri* although sprout production for both species appears somewhat season-dependant. From these results it appears that prescribed fire in early spring or late fall has minimal effect on sprouting response. Disturbance during the growing season (June or July) appears to have a negative effect on sprout production for both species. As additional programs are established to restore ecological function in ponderosa pine forest ecosystems, further research should examine responses of other important understory species to fire behavior.

Management activities that facilitate growth and retention of large *C. fendleri* stems can increase seed inputs to soil seed banks. Protecting plants from intense ungulate herbivory may allow rapid development of large fruit-producing stems. Gross fruit production as an indicator of viable seed inputs may be misleading since ovule and seed losses from abortion and predispersal parasitism can be high. Rapid estimates of viable seeds can be made by examination of mature fruit contents before dehiscence. A subsample of normal appearing seeds should be dissected to determine degree of parasitism. Managers also should note that seed predators may consume a significant proportion of dispersed seeds. *C. fendleri* flower, fruit, and seed use by various organisms demonstrates the importance of each of this species' reproductive stages in contributing to overall ecosystem function.

Results of our studies demonstrate that *C. fendleri* and *R. woodsii* are integral components of ponderosa pine forest ecosystems. Both species provide important habitat qualities for a myriad of organisms within the food web. Species utilizing these shrubs ranged from large herbivores like mule deer and elk, to seed eaters such as rodents and birds, to insects such as parasitic wasps. Short-term responses of *C. fendleri* and *R. woodsii* to forest restoration and fuels management treatments were generally positive; plants were rejuvenated through new sprout development; reproductive processes, such as flower production and seedling establishment, that did not occur in untreated forest units, were observed for *C. fendleri*. Thus, restorative treatments such as tree thinning to reduce wildfire hazard and competitive effects on understory communities, and applications of prescribed fire to reduce accumulated fuel loads and reintroduce a critical ecosystem process, by enhancing growth and reproduction of important plant species such as *Ceanothus fendleri* and *Rosa woodsii*, help to return ecological function to these forests.

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## Literature Cited

- Allen, C.D. 1996. Elk response to the La Mesa fire and current status in the Jemez mountains. pp.179-195 in Allen, C.D. (ed.), Proceedings of the 2nd La Mesa Fire Symposium. USDA Forest Service General Technical Report RM-GTR-286, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, USA.
- Andariese, S.W., and W.W. Covington. 1986. Changes in understory production for three prescribed burns of different ages in ponderosa pine. *Forest Ecology and Management* 14:193-203.
- Anderson, R.C., and O.L. Loucks. 1979. White-tail deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. *Journal of Applied Ecology* 16:855-861.
- Arnold, J.F. 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. *Journal of Forestry* 48:118-126.
- Augustine, D.J., and L.E. Frelich. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. *Conservation Biology* 12:995-1004.
- Augustine, D.J., and S.J. Mc Naughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62:1165-1183.
- Austin, D.D., and A.B. Hash. 1988. Minimizing browsing damage by deer: landscaping planning for wildlife. *Utah Science* 49:66-70.
- Avery, T.E., and H.E. Burkhardt. 1983. Forest measurements. McGraw-Hill Book Co., New York, New York. USA.
- Baines, D., R.B. Sage, and M.M. Baines. 1994. The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. *Journal of Applied Ecology* 31:776-783.
- Biondi, F. 1996. Decadal-scale dynamics at the Gus Pearson Natural Area: evidence for inverse asymmetric competition? *Canadian Journal of Forest Research* 26:1397-1406.
- Blauer, A.C., A.P. Plummer, E.D. McArthur, R. Stevens, and B.C. Giunta. 1975. Characteristics and hybridization of important intermountain shrubs. I. Rose family. USDA Forest Service Research Paper INT-169.
- Bojorquez Tapia, L.A., P.F. Ffolliott, and D.P. Guertin. 1990. Herbage production-forest overstory relationships in two Arizona ponderosa pine forests. *Journal of Range Management* 43:25-28.
- Borror, D.J., C.A. Triplehorn, and N.F. Johnson. 1989. Introduction to the study of insects. Thompson Learning, Inc., Toronto, Ontario, Canada.
- Brender, E.V., and R.W. Copper. 1968. Prescribed burning in Georgia's Piedmont loblolly pine stands. *Journal of Forestry*, 66: 31-36.
- Brown, J.K., and N.V. DeByle. 1989. Effects of prescribed fire on biomass and plant succession in western aspen. USDA Forest Service Research Paper INT-412.
- Buckman, R.E. 1964. Effects of prescribed burning on hazel in Minnesota. *Ecology*, 45: 626-629.
- Bugbee, R.E. 1967. Revision of chalcid wasps of genus *Eurytoma* in America, north of Mexico. *Proceedings of the United States National Museum* 118:433-532.
- Bugbee, R.E. 1971. A new species of Arizona *Eurytoma* phytophagous in *Ceanothus greggii* seeds. *Journal of the Kansas Entomological Society* 44:111-112.



- Conard, S.G., A.E. Jaramillo, K. Cromack Jr., and S. Rose. 1985. The role of the genus *Ceanothus* in western forest ecosystems. USDA Forest Service General Technical Report PNW-182.
- Covington, W.W. and S.S. Sackett. 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. *Forest Science* 30:183-192.
- Covington, W.W., and S.S. Sackett. 1990. Fire effects on ponderosa pine soils and their management implications. Pp105-111 in Krammes, J.S. (Tech Coord.), Effects of fire management of southwestern natural resources. USDA Forest Service General Technical Report RM-191.
- Covington, W.W., and M.M. Moore. 1994a. Southwestern ponderosa forest structure and resource conditions: changes since Euro-American settlement. *Journal of Forestry* 92:39-47.
- Covington, W.W., and M.M. Moore. 1994b. Postsettlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forests. *Journal of Sustainable Forestry* 2:153-181.
- Covington, W.W., P.Z. Fulé, M.M. Moore, S.C. Hart, T.E. Kolb, J.N. Mast, S.S. Sackett, and M.R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. *Journal of Forestry* 95:23-29.
- Devore, J., and R. Peck. 1986. Statistics – the exploration and analysis of data. West Publishing Co. St. Paul, MN, USA.
- Dunlap, T.R. 1988. That Kaibab myth. *Journal of Forest History* 32:60-68.
- Ferguson, E.R. 1957. Stem-kill and sprouting following prescribed fires in a pine-hardwood stand in Texas. *Journal of Forestry* 55: 426-429.
- Ffolliott, P.F., and W.P. Clary. 1975. Differences in herbage-timber relationships on sedimentary and igneous soils in Arizona ponderosa pine stands. *Progressive Agriculture in Arizona* 27:6-7.
- Ffolliott, P.F., W.P. Clary, and F.R. Larson. 1977. Effects of a prescribed fire in an Arizona ponderosa pine forest. USDA Forest Service Research Note RM-336.
- Fulé, P.Z., W.W. Covington, and M.M. Moore. 1997. Determining reference conditions for ecosystem management in southwestern ponderosa pine forests. *Ecological Applications* 7:895-908.
- Fulé, P.Z., C. McHugh, T.A. Heinlein, and W.W. Covington. 2001a. Potential fire behavior is reduced following forest restoration treatments. pp. 28-35 in Vance, R.R., C.B. Edminster, W.W. Covington, and J.A. Blake (comps.), *Ponderosa pine ecosystems restoration and conservation: steps toward stewardship*. USDA Forest Service Proceedings RMRS-P-22.
- Fulé, P.Z., A.E.M. Waltz, W.W. Covington, and T.A. Heinlein. 2001b. Measuring forest restoration effectiveness in reducing hazardous fuels. *Journal of Forestry* 99:24-29.
- Fulé, P.Z., W.W. Covington, H.B. Smith, J.D. Springer, T.A. Heinlein, K.D. Huisinga, and M.M. Moore. 2002. Comparing ecological restoration alternatives: Grand Canyon, Arizona. *Forest Ecology and Management* 170:19-41.
- Furniss, M.M., and R.G. Krebill. 1972. Insects and diseases of shrubs on western big game ranges. pp. 218-226 in McKell, C.M., J.P. Blaisdell, and J.R. Goodin (Tech. Eds.) *Wildland shrubs – their biology and utilization*. USDA Forest Service General Technical Report INT-1.
- Furniss, M.M., T.A. Leege, and R.J. Naskali. 1978. Insects that reduce redstem *Ceanothus* seed production in Idaho. In: *Proceedings of the First International Rangeland Congress*
- Gill, J.D., and F.L. Pogge. 1974. *Rosa* L. pp. 732-737 in Schopmeyer, C. S. (tech. coord.), *Seeds of Woody Plants*. USDA Handbook 450.
- Gratkowski, H. 1974. Origin of mountain whitethorn brushfields on burns and cuttings in Pacific Northwest forests. *Western Society of Weed Science Proceedings* 27:5-8.
- Hadley, E.B. 1961. Influence of temperature and other factors on *Ceanothus megacarpus* seed germination. *Madroño* 16:132-138.
- Harrington, M. G. 1985. The effects of spring, summer, and fall burning on Gambel oak in a Southwestern ponderosa pine stand. *Forest Science* 31: 156-163.
- Hoffman, T.L., and C.L. Wambolt. 1996. Growth response of Wyoming big sagebrush to heavy browsing by wild ungulates. pp. 242-245 in Barrow, J.R., E.D. McArthur, R.E. Sosebee, R.J. Tausch (comps.), *Proceedings: Shrubland ecosystem dynamics in a changing environment*. USDA Forest Service General Technical Report INT-GTR-338, Intermountain Research Station, Ogden, UT, USA.



- Hogg, E.H., and V.J. Lieffers. 1991. The relationship between seasonal changes in rhizome carbohydrate reserves and recovery following disturbance in *Calamagrostis canadensis*. *Canadian Journal of Botany*, 69: 641-646.
- Huffman, D.W., J.C. Tappeiner II, and J.C. Zasada. 1994. Regeneration of salal (*Gaultheria shallon*) in the central Coast range forests of Oregon. *Canadian Journal of Botany* 72:39-51.
- Huffman, D.W. 2002. A seed chalcid (*Eurytoma squamosa* Bugbee) parasitizes seeds of buckbrush (*Ceanothus fendleri* Gray) in a ponderosa pine forest of Arizona. *Western North American Naturalist* 62:474-478.
- Huffman, D.W., and M.M. Moore. 2003. Ungulate herbivory on buckbrush in an Arizona ponderosa pine forest. *Journal of Range Management In Press*.
- Jackson, L.L., N. Lopoukhine, and D. Hillyard. 1995. Commentary ecological restoration: a definition and comments. *Restoration Ecology* 3:71-75.
- Kauffman, J.B., and R.E. Martin. 1990. Sprouting shrub response to different seasons and fuel consumption levels of prescribed fire in Sierra Nevada mixed conifer ecosystems. *Forest Science* 36:748-764.
- Kay, C.E. 1997. Is aspen doomed? *Journal of Forestry* 95:4-11.
- Kearney, T. H., and R. H. Peebles. 1964. Arizona flora. University of California Press, Los Angeles, CA, USA.
- Keeley, J.E. 1977. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. *Ecology* 58:820-829.
- Keeley, J.E. 1987. Fruit production patterns in the chaparral shrub *Ceanothus crassifolius*. *Madroño* 34:273-282.
- Keeley, J.E. 1992. Recruitment of seedlings and vegetative sprouts in unburned chaparral. *Ecology* 73:1194-1208.
- Kolb, T.E., M.R. Wagner, and W.W. Covington. 1994. Concepts of forest health. *Journal of Forestry* 92:10-15.
- Krishnan, S. 1989. Propagation of four native drought tolerant shrubs -- *Ceanothus* spp. and *Sherpherdia* spp. Thesis. Colorado State University, Fort Collins, CO, USA.
- Kuel, R.O. 1994. Statistical principles of research design and analysis. Wadsworth Publishing Co. Belmont, CA, USA.
- Kurmis, V., and E. Sucoff. 1991. Population density and height distribution of *Corylus cornuta* in undisturbed forests of Minnesota: 1965-1984. *Canadian Journal of Botany* 67:2409-2413.
- Landhäusser, S. M., and Lieffers, V. J. 1997. Seasonal changes in carbohydrate storage and regrowth in rhizomes and stems of four boreal forest shrubs: applications in *Picea glauca* understory regeneration. *Scandinavian Journal of Forest Research*, 27-32.
- Lotti, T. 1956. Eliminating understory hardwoods with summer prescribed fires in coastal plain loblolly pine stands. *Journal of Forestry* 54:191-192.
- Mast, J.Y., P.Z. Fulé, M.M. Moore, W.W. Covington, and A.E.M. Waltz. 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. *Ecological Applications* 9:228-239.
- Menke, J. W., and Trlica, M. J. 1981. Carbohydrate reserve, phenology, and growth cycles of nine Colorado range species. *Journal of Range Management*, 34: 269-277.
- Meurisse, R. T. 1971. Soil Report on the San Francisco Peaks Area – Elden and Flagstaff Ranger Districts, Coconino National Forests. USDA Forest Service (unpublished).
- Mills, J.N., and J. Kummerow. 1989. Herbivores, seed predators, and chaparral succession. pp. 49-53 in Keeley, S.C. (ed) *The California chaparral – paradigms reexamined*. Science Series No. 34. Natural History Museum, Los Angeles, CA, USA.
- Mitchell, J. E., and D. R. Freeman. 1993. Wildlife-livestock-fire interactions on the North Kaibab: A historical review. USDA Forest Service, General Technical Report, RM-222, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Moore, M.M., and D.A. Dieter. 1992. Stand density index as a predictor of forage production in northern Arizona pine forests. *Journal of Range Management* 45:267-271.
- Moore, M.M., W.W. Covington, and P.Z. Fulé. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecological Applications* 9:166-1277.
- Morgan, P., and L.F. Neuenschwander. 1988. Seed bank contributions to regeneration of shrubs species and clear-cutting and burning. *Canadian Journal of Botany* 66:169-172.

- Naiman, R.J. 1988. Animal influences on ecosystem dynamics (Large animals are more than passive components of ecological systems). *Bioscience* 38:750-752.
- Noste, N.V. 1985. Influence of fire severity on response of evergreen *Ceanothus*. In: *Fire Effects of Wildlife Habitat Symposium Proceedings* USDA Forest Service INT-186.
- Opperman, J.J., and A.M. Merenlender. 2000. Deer herbivory as an ecological constraint to restoration of degraded riparian corridors. *Restoration Ecology* 8:41-47.
- Paige, K.N. and T.G. Whitham. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. *The American Naturalist* 129:407-416.
- Patton, D.R. 1974. Patch cutting increases deer and elk use of a pine forest in Arizona. *Journal of Forestry* 72:764-766.
- Pearson, H.A., J.R. Davis, and G.H. Schubert. 1972. Effects of wildfire on timber and forage production in Arizona. *Journal of Range Management* 25:250-253.
- Pyne, S.J., P.L. Andrews, and R.D. Laven. 1996. *Introduction to wildland fire*. John Wiley and Sons, Inc. New York, New York, USA.
- Quick, C.R. 1935. Notes on the germination of *Ceanothus* seeds. *Madroño* 3:135-140.
- Quick, C.R., and A.S. Quick. 1961. Germination of *Ceanothus* seeds. *Madroño* 16:23-31.
- Reed, M.J. 1974. *Ceanothus* L. *Ceanothus*. pp. 284-290 in Schopmeyer C.S. (Tech Cord), *Seeds of woody plants in the United States*. USDA Forest Service Handbook No. 450.
- Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. *Journal of Agriculture Research* 46:627-638.
- Reynolds, H.G. 1964. Effect of logging on understory vegetation and deer use in a ponderosa pine forest of Arizona. *USDA Forest Service Research Note* 80.
- Rosenthal, J.P., and P.M. Kotanen. 1994. Terrestrial plant tolerance to herbivory. *Trends in Ecology and Evolution* 9:145-148.
- Savage, M., P.M. Brown, and J. Feddema. 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. *Ecoscience* 3:310-318.
- Society for Ecological Restoration. 1993. *Mission statement*, Society for Ecological Restoration. *Restoration Ecology* 1:206-207.
- Stein, S.J., P.W. Price, W.G. Abrahamson, and C.F. Sacchi. 1992. The effect of fire on stimulating willow regrowth and subsequent attack by grasshoppers and elk. *Oikos* 65:190-196.
- Stephenson, A.G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* 12:253-279.
- Story, M.T. 1974. Nitrogen fixation by *Ceanothus fendleri* and *Lupinus argenteus* as a function of parent material and vegetal cover. Thesis. University of Arizona, Tucson, Arizona, USA.
- Strohmeyer, S., and J. Maschinski. 1996. Cattle and elk herbivory on Arizona willow (*Salix arizonica*). pp. 187-192 in Maschinski, J., H. D. Hammond, and L. Holter (tech. coords.), *Southwestern rare and endangered plants: Proceedings of the second conference*. USDA Forest Service General Technical Report RM-GTR-283, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Suzuki, K., H. Suzuki, D. Binkley, and T. Stohlgren. 1999. Aspen regeneration in the Colorado Front Range: differences at local and landscape scales. *Landscape Ecology* 14:231-237.
- Tappeiner, J.C. II, J.C. Zasada, D.W. Huffman, and L.M. Ganio. 2001. Salmonberry and salal annual aerial stem production: the maintenance of a shrub cover in forest stands. *Canadian Journal of Forest Research* 31:1629-1638.
- Throop, H.L., and P.A. Fay. 1999. Effects of fire, browsers, and gallers on New Jersey tea (*Ceanothus herbaceous*) growth and reproduction. *American Midland Naturalist* 141:51-58.
- Trlica, M.J., and Cook, C.W. 1971. Defoliation effects on carbohydrate reserves of desert species. *Journal of Range Management*, 24:418-425.
- Truett, J. 1996. Bison and elk in the American Southwest: In search of the pristine. *Environmental Management* 20:195-206.
- Urness, P. J., D. J. Neff, and R. K. Watkins. 1975. Nutritive value of mule deer forages on ponderosa pine summer range in Arizona. *USDA Forest Service Research Note* RM-304.

- Uresk, D.W., and K.E. Severson. 1989. Understory-overstory relationships in ponderosa pine forests, Black Hills, South Dakota. *Journal of Range Management* 42:203-208.
- USDI 1992. Western Region Fire Monitoring Handbook. Western Region Prescribed and Natural Fire monitoring Task Force. United States Department of Interior National Park Service, San Francisco, CA.
- Vose, J.M., and A.S. White. 1987. Process of understory seedling recruitment 1 year after prescribed fire in an Arizona ponderosa pine community. *Canadian Journal of Botany* 65:2280-2290.
- Vose, J.M., and A.S. White. 1991. Biomass response mechanisms of understory species the first year after prescribed burning in an Arizona ponderosa pine community. *Forest Ecology and Management* 40:175-187.
- Waltz, A.E.M. 2001. Butterfly response to ponderosa pine restoration and the efficacy of butterflies as indicators of pollinators. Dissertation. Northern Arizona University, Flagstaff, AZ.
- Welch, B.L., and D. Andrus. 1977. Rose hips -- a possible high-energy food for wintering mule deer? USDA Forest Service Research Note INT-221.
- Western Regional Climate Center. 2003. Western U.S. historical climate summaries. Flagstaff Airport, Flagstaff, AZ. <http://www.wrcc.dri.edu/climsum.html>.
- Whelan, R.J. 1995. The ecology of fire. Cambridge University Press, Cambridge, UK.
- Young, D.L., and J.A. Bailey. 1975. Effects of fire and mechanical treatment on *Cercocarpus montanus* and *Ribes cereum*. *Journal of Range Management*, 28:495-497.
- Zammit, C.A., and P.H. Zedler. 1992. Size structure and seed production in even-aged populations of *Ceanothus greggii* in mixed chaparral. *Journal of Ecology* 81:499-511.
- Zasada, J.C., J.C. Tappeiner III, B.D. Maxwell, and M.A. Radwan. 1994. Seasonal changes in shoot and root production and in carbohydrate content of salmonberry (*Rubus spectabilis*) rhizome segments from the central Oregon Coast Ranges. *Canadian Journal of Forest Research*, 24:272-277.